PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Research

Cite this article: Huxley PJ, Murray KA, Pawar S, Cator LJ. 2021 The effect of resource limitation on the temperature dependence of mosquito population fitness. *Proc. R. Soc. B* **288**: 20203217.
https://doi.org/10.1098/rspb.2020.3217

Received: 30 December 2020
Accepted: 31 March 2021

Subject Category:
Ecology

Subject Areas:
ecology, health and disease and epidemiology, systems biology

Keywords:
climatic warming, abundance, temperature, population fitness, resource limitation, vector-borne disease

Author for correspondence:
Paul J. Huxley
e-mail: p.huxley@imperial.ac.uk

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.5372468.

THE ROYAL SOCIETY PUBLISHING

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

Paul J. Huxley[1], Kris A. Murray[1,2], Samraat Pawar[3] and Lauren J. Cator[3]

[1]MRC Centre for Global Infectious Disease Analysis, School of Public Health, Imperial College London, London, UK
[2]MRC Unit The Gambia at London School of Hygiene & Tropical Medicine, Banjul, The Gambia
[3]Department of Life Sciences, Imperial College London, Ascot, UK

PJH, 0000-0001-9211-9479; KAM, 0000-0002-8382-0674; SP, 0000-0001-8375-5684; LJC, 0000-0002-6627-1490

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, partially by affecting abundance dynamics of the vector population. These temperature–trait relationships are typically estimated from juvenile 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 modelling, we show that low-resource supply in the juvenile life stages 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 a decrease in adult size with temperature at low-resource supply. Our study suggests that most projections of temperature-dependent vector abundance and disease transmission are likely to be biased because they are based on traits measured under optimal resource supply. Our results provide compelling evidence for future studies to consider resource supply when predicting the effects of climate and habitat change on vector-borne disease transmission, disease vectors and other arthropods.

1. Introduction

The global burden of human, animal and plant vector-borne diseases has increased substantially in recent decades [1,2]. The transmission patterns of these diseases are strongly linked to the spatiotemporal distributions and abundances of their vectors [3,4]. Therefore, there is growing concern that climate and land-use change coupled with rapid globalization may shift the distributions and abundances of vector species, and thus, the diseases they transmit [5,6]. However, we currently lack a mechanistic understanding of how changes in multiple environmental drivers interact to affect the abundance of disease vectors [7–9].

Because most disease vectors are small ectotherms, environmental temperature in particular can have large effects on their population fitness [5,6,10–15]. Many biological rates (including metabolic, development and fecundity rate [7]) of ectotherms increase approximately exponentially with temperature up to some optimum before declining to a baseline [16]. A number of recent studies have used laboratory data on the thermal responses of functional traits of vectors to predict how temperature will affect vector abundance and disease transmission in the field, leading to new insights, including a much lower optimal temperature for malaria transmission than previously thought [17]. However, these laboratory-derived temperature–trait relationships are generally measured in populations reared on optimal resource supply, whereas natural vector

populations are expected to experience variation in resource supply, including intermittent resource limitation.

Indeed, along with temperature, resource supply is another ubiquitous environmental driver that is expected to limit the fitness of vector populations in nature [18–20]. Moreover, temperature and resource supply are expected to act interactively [9,21]. The primary reason for this prediction is that while the energy cost of somatic maintenance, growth and ontogenetic development of individuals generally increases with temperature [22,23], the ability to meet this increasing demand depends on resource supply. If the resources available to an individual do not keep pace with increasing energy requirements, its growth, development and survival would be compromised. This resource limitation should negatively affect fitness, with the severity of these effects increasing with temperature. While the importance of resource supply in mediating the effect of temperature on population abundance may seem obvious, this problem remains largely unresolved theoretically and empirically, not just in vector-borne disease research, but in thermal ecology in general. For example, ecological metabolic theories (including the metabolic theory of ecology (MTE) and dynamic energy budget (DEB) theory), which seek to link organismal metabolic rates to ontogenetic and population growth, generally assume that external resource supply is not a limiting factor [22–25].

Resource supply can also interact with temperature to affect the population fitness of ectotherms by determining size at maturity. Generally, size at maturity decreases with rising temperature (the size–temperature rule [26], which also applies to disease vectors, such as mosquitoes [27]). The size–temperature rule also remains largely untested under resource limitation in disease vectors and other ectotherms [26,28]. For vectors specifically, female size is demographically and epidemiologically important because it is associated with longevity, fecundity and biting behaviour [29,30].

In general, the question of whether and how temperature and resource supply interact to modulate disease transmission together through effects on underlying traits remains open. Here, we seek to address this gap in knowledge by investigating the effect of realistic variation in resource supply on the temperature dependence of population-level fitness in *Aedes aegypti*, a principal mosquito vector of human arboviruses (e.g. dengue, yellow fever and Zika; [31]). Because resource competition between larvae is expected to be a major regulator of adult mosquito abundance, many studies have examined how resource supply and larval density interact to affect fitness [32–35], while others have investigated the effect of resource supply and larval density separately [36,37]. However, none of these studies considered environmental temperature. On the other hand, studies that have considered temperature have not examined how the effects of temperature and resource supply on underlying fitness traits can propagate through the system to affect population fitness [38,39]. By taking a trait-based approach, we seek to gain general, mechanistic insights into how resource availability and temperature may together affect the abundance of disease vectors and other arthropods in the field.

2. 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 [40] that this strain of *Ae. aegypti* is likely to experience in the wild (F16–19 originating from Fort Meyer, FL; [41]). Our low-resource supply level was chosen because previous work has found that it is the highest resource limitation that can be applied to this species without resulting in complete juvenile mortality [18,19]; a level of limitation that might be expected in wild populations. We also determined that the low-resource level was appropriate with a preliminary assay (electronic supplementary material, tables S4 and S5). The high-resource supply level corresponds to the upper mid-range of the high-resource supply levels used in Arrivillaga & Barrera [18] and Barrera *et al.* [19] and is consistent with the levels of resource supply commonly used in laboratory studies on this species [38,42].

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 dechlorinated 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 12 L : 12 D photoperiod and 30 min 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). We conducted a preliminary assay to determine the adequacy of this replication level to detect statistically significant effect sizes (electronic supplementary material, tables S4 and S5). Low-resource supply treatments were provided 3 mg of 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 stages. 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}). Electronic supplementary material, figure S1 is a schematic of the experimental design and the traits measured.

(a) Fitness calculation

To calculate population-level fitness, we used our data to parameterize stage-structured matrix projection models [43], which describe a change in a population over time:

$$\boldsymbol{N}_{t+1} = \boldsymbol{M}\boldsymbol{N}_t, \tag{2.1}$$

where $\boldsymbol{N}_t$ is a vector of abundances in the stage classes at time t and $\boldsymbol{M}$ is the population projection matrix. The first row of $\boldsymbol{M}$ is populated by daily fecundity (the number of female offspring produced per female at age i). The sub-diagonal of $\boldsymbol{M}$ is populated with the proportions of survival from age i to age i+1. Multiplying the transition matrix ($\boldsymbol{M}$; equation (2.1)) and stage-structured population size vector ($\boldsymbol{N}_t$) sequentially across time intervals yields the stage-structured population dynamics. Once the stable stage distribution of the abundance vector is reached, the dominant eigenvalue of the system is the finite population rate of increase (λ) [43]. Then, the intrinsic rate of population growth is

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

This is a population's inherent capacity to reproduce and therefore a measure of population-level fitness [24,44,45]. Negative

r_{max} values indicate decline and positive ones, growth. The projection matrices were built and analysed using the popbio R package [46,47].

(b) Parameterization

(i) Immature development time and immature and adult survival proportions

Matrix survival elements (the sub-diagonal of the matrix $\boldsymbol{M}$; equation (2.1)) were populated with continuous survival proportions estimated using the Kaplan–Meier survival function in the survival R package [46,48]. 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 5 ml of tap water. This enabled pupa-to-adult development durations and the lifespans of individual starved adults to be recorded. Starvation forces adults to metabolize nutritional reserves accumulated during larval development, so starved lifespan should increase with body size. Therefore, starved adult lifespan is a useful indicator of the carry over effects of temperature and resource availability in the larval habitat [49,50].

(ii) Daily fecundity rate

The use of scaling relationships between fecundity and size is common in predictions of population growth in *Aedes* mosquitoes [51,52]. A detailed description of our method for estimating fecundity is provided in the electronic supplementary material (electronic supplementary material, figure S2). Briefly, we measured wing length as a proxy for body size, and estimated lifetime fecundity using previously published datasets on the temperature- and resource supply-dependent scaling between wing length and lifetime fecundity [42,50]. Daily fecundity rate is required for the first row of $\boldsymbol{M}$ (equation (2.1)), so lifetime fecundity was divided by lifespan and multiplied by 0.5 (assuming a 1 : 1 male-to-female offspring ratio) to give temperature-specific individual daily fecundity.

(c) Parameter sensitivity

We used the delta method to approximate 95% confidence intervals (CIs) for our fitness calculations [43,53] 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 in the survival R package. For fecundity, we calculated the standard errors of the mean daily fecundity rates (electronic supplementary material, table S2) for each treatment using the Rmisc R package [54]. As an additional sensitivity analysis, we recalculated fitness using the upper and lower 95% CIs of the exponents for the scaling of wing length and lifetime fecundity (figure 3; electronic supplementary material, figure S2).

(d) 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 $\boldsymbol{M}$ (equation (2.1)) with all other elements held constant (the partial derivative) [55,56]. This partial derivative of λ, with respect to each element of $\boldsymbol{M}$, is $s_{ij} = \partial\lambda/\partial a_{ij} = v_i w_j$ with the dot product $\langle \boldsymbol{w}, \boldsymbol{v} \rangle = 1$. Here, $\boldsymbol{w}$ is the dominant right eigenvector (the stage distribution vector of $\boldsymbol{M}$), $\boldsymbol{v}$ is the dominant left eigenvector (the reproductive value vector of $\boldsymbol{M}$) and a_{ij} is the $i \times j$th element of $\boldsymbol{M}$. 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 [55,56]. Absolute contributions for juvenile and adult elements were summed and changed proportionally to quantify the sensitivity of r_{max} to these traits.

(e) Statistical analyses

All statistical analyses were conducted using R [46]. 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 responses of development time, lifespan and wing length. Replicate was included in these GLMs as a fixed effect.

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 [57]. The Gompertz survival function was the best fit to these data according to the Akaike information criterion (AIC) (electronic supplementary material, 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 worsened model fit (ΔAIC > −2), then it was retained. Otherwise, it was removed (electronic supplementary material, table S3). For each treatment, maximum-likelihood methods executed in flexsurv estimated the 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. These parameter estimates were then used to determine the significance of the effects of temperature and resource supply on juvenile mortality.

3. Results

All trait responses varied significantly with temperature and resource supply, with a significant interaction between the two environmental variables (figures 1 and 2; electronic supplementary material, tables S1 and S2). Thus, the realized effect of temperature on trait responses was consistently and significantly mediated by resource supply.

At a low-resource supply, daily juvenile mortality rates, μ_x, increased with time at all temperatures, whereas at high-resource supply, they decreased with time (figure 1*e*). 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; figure 1*c*). 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; figure 1*d*).

Development time varied significantly with the interaction between temperature and resource supply (ANOVA; $F_{2,0.75} = 24.11$, $p < 0.001$; electronic supplementary material, table S1). Whereas development time decreased both at warmer temperatures and at high-resource supply, the decrease with temperature was greater at low-resource supply than at high-resource supply. At low-resource supply, development time decreased by 15.45 days as temperatures increased from 22 to 32°C, whereas at high-resource supply, it decreased by 6.38 days across this range (figure 2*a*; electronic supplementary material, table S2).

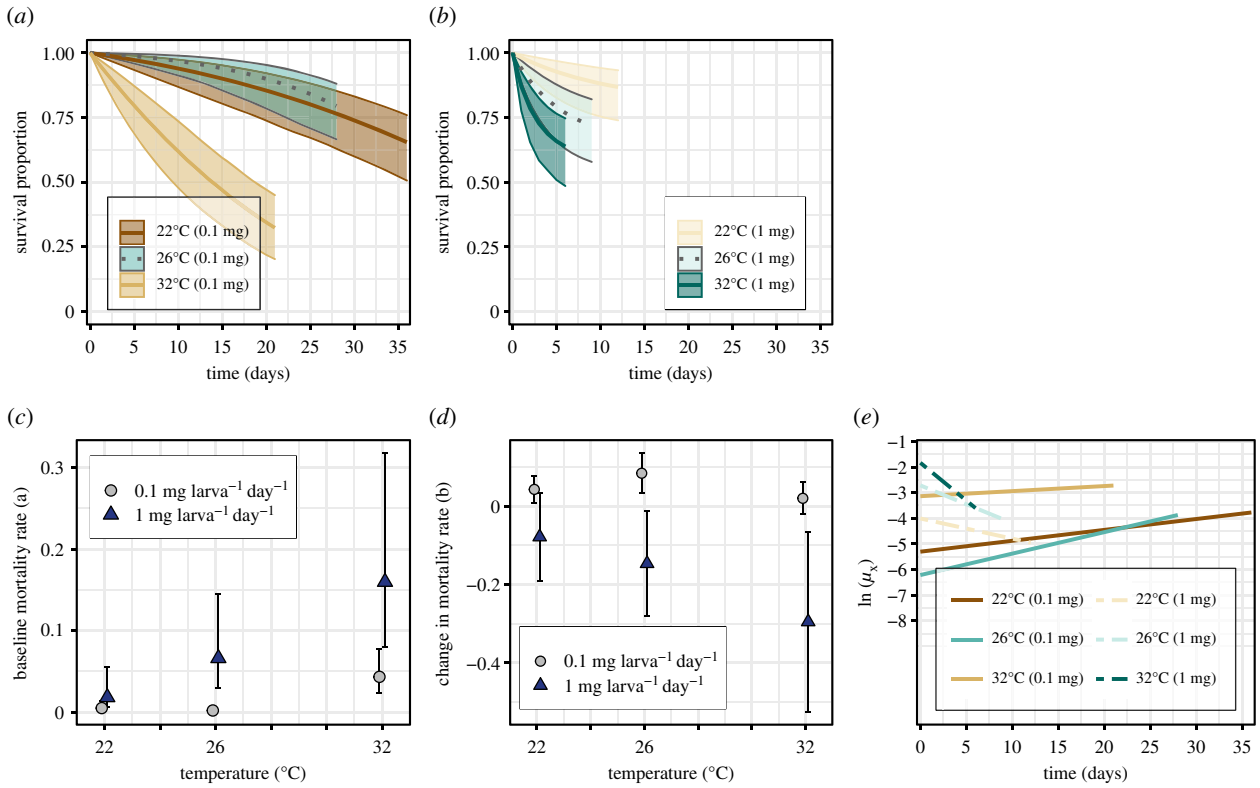

Figure 1. The effect of resource supply on the temperature dependence of juvenile survival. Survival curves at (*a*) low- and (*b*) high-resource supply by temperature with 95% confidence bounds. Predicted survival for each treatment was 22°C at low-resource supply = 65%, at high-resource supply = 87%; 26°C at low-resource supply = 80%, at high-resource supply = 83%; 32°C at low-resource supply = 32%, at high-resource supply = 0.64%. (*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 22°C (95% CIs at 26 and 32°C do not overlap). (*e*) Logged daily mortality rates ($\ln(\mu_x) = \ln(a) + bx$) show how mortality rates at low-resource supply started low and increased with time; at high-resource supply, they started high and decreased with time.

Adult lifespan varied significantly with the interaction between temperature and resource supply (ANOVA; $F_{2,\ 2.41} = 14.95$, $p < 0.001$; electronic supplementary material, table S1). Although lifespan decreased both at warmer temperatures and at low-resource supply, the 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 (figure 2*b*; electronic supplementary material, table S2).

The interaction between temperature and resource supply resulted in significant variation in size at maturity (wing length) between resource levels (ANOVA; $F_{2,0.03} = 4.36$, $p = 0.01$; electronic supplementary material, table S1). Adult size decreased both at warmer temperatures and at low-resource supply, though the decrease with temperature was greater at high-resource supply than at low-resource supply. As temperatures increased from 22 to 32°C, size decreased by 0.54 mm at high-resource supply, whereas size at low-resource supply decreased by 0.37 mm (figure 2*c*; electronic supplementary material, table S2).

(a) Population fitness (r_{max})

Resource limitation depressed r_{max} to negative values at all temperatures, with a unimodal relationship of r_{max} with temperature (figure 3; electronic supplementary material, 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. By contrast, at high-resource supply, r_{max} was always positive and increased with temperature from 0.17 at 22°C to maximal growth (0.28) at 32°C.

(b) Elasticity analysis

Juvenile development and survival were the most important contributors to r_{max} (electronic supplementary material, figure S3). For example, at low-resource supply at 32°C, a 0.5 proportional increase in juvenile traits would almost halve the rate of decline from −0.380 to −0.202 (electronic supplementary material, figure S3a). By contrast, for the same treatment, a proportional increase of the same magnitude for adult survival would increase r_{max} from −0.380 to −0.376 (electronic supplementary material, figure S3c), and fecundity would increase r_{max} from −0.380 to −0.372 (electronic supplementary material, figure S3d). 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.

4. Discussion

Our results show that juvenile resource regimes can have far-reaching effects on the temperature dependence of

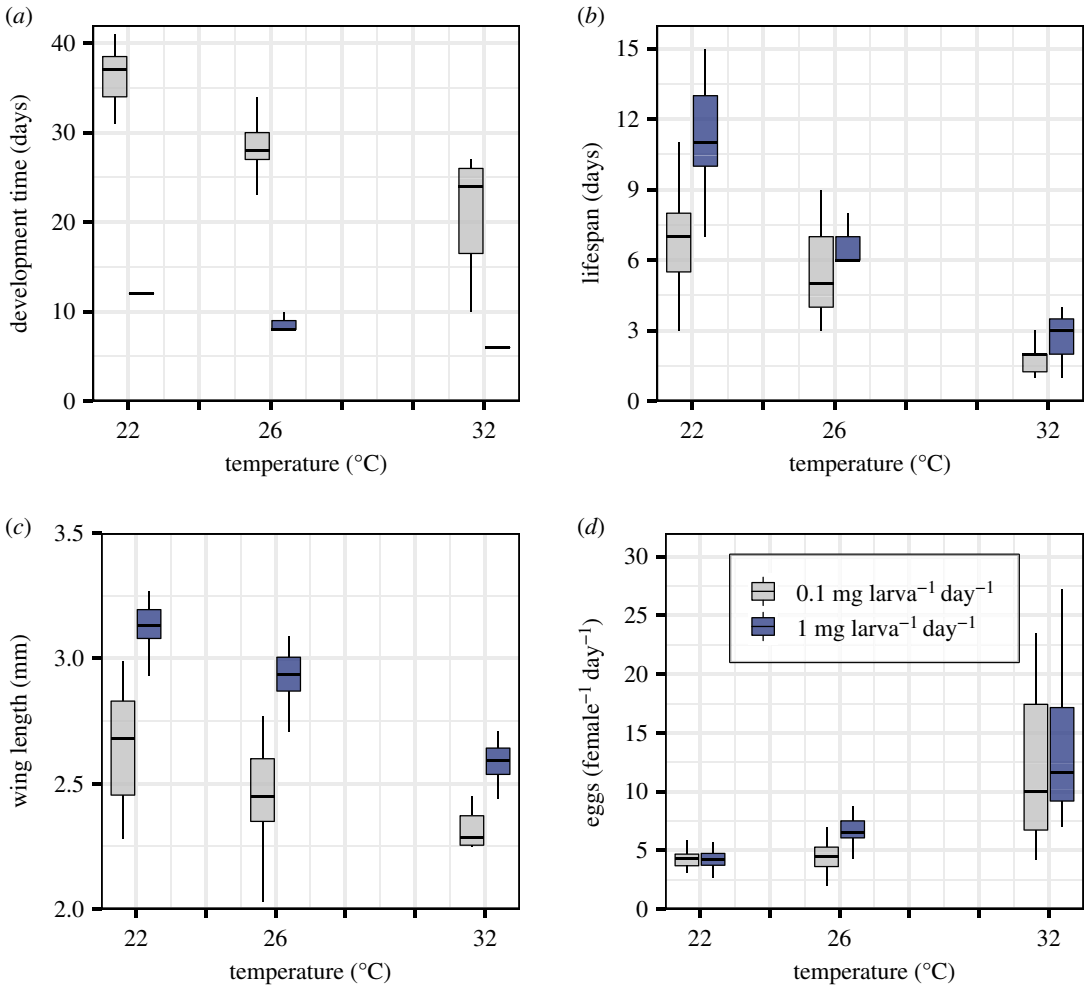

Figure 2. The combined effect of temperature and resource supply level on *Ae. aegypti* life-history traits. (*a–c*) Resource supply significantly modulated the effect of temperature on all directly measured traits, except adult lifespan at 26°C (*b*). The resulting ANOVAs of the GLMs for each trait are presented in the electronic supplementary material, table S1. The GLM-estimated trait means with 95% CIs calculated from the standard errors are shown in the electronic supplementary material, table S2. (*d*) Predicted fecundity increased significantly with the 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 $n = 27$. Boxplot horizontal lines represent medians. Lower and upper hinges are the 25th and 75th percentiles. Upper whiskers extend from the hinge to the largest value no further than 1.5 × inter-quartile range (IQR) from the hinge. The lower whisker extends from the hinge to the smallest value at most 1.5 × IQR of the hinge.

population-level fitness, r_{max}. Differences between the thermal response of traits at low- versus high-resource supply resulted in a marked divergence of the temperature dependence of r_{max} between the two resource levels (figure 3). At low-resource supply, fitness was negative for all three temperatures tested and was much lower at 32°C than 26°C. This indicates that population fitness becomes increasingly and nonlinearly constrained by resource limitation as temperatures increase. By contrast, fitness at high-resource supply was positive and increased moderately from 26°C to 32°C. While recent studies show that interactions between temperature and resource availability can mediate population growth in single-celled plankton [21,58,59], studies of how such interactions can affect eukaryotes are rare (but see [87]). Our study shows that the effects of temperature × resource availability interactions need to be considered to accurately predict and understand how natural disease vector populations and other arthropods will respond to environmental change.

The elasticity analysis (electronic supplementary material, figure S3) shows that the primary mechanism underlying the divergent temperature dependence of r_{max} across resource levels is decreased juvenile survival and increased juvenile development time at low resources. Population-level reproductive output decreased at low resources because decreased juvenile survival (figure 1) reduced the number of reproducing individuals, and increased juvenile development time (figure 2*a*) delayed the onset of reproduction. At low-resource supply, the daily mortality rate started low and then increased over time, while at high-resource supply, it started high and then decreased to very low levels (figure 1*e*). Resource limitation substantially increased development time at all temperatures (figure 2*a*).

Fecundity and adult lifespan had comparatively negligible effects on r_{max}, which suggests that the carry over effect of reduced size at maturity on r_{max} is relatively weak. For example, at high-resource supply, adult lifespan and body size were greater at 26°C than at 32°C, yet fitness at 32°C was predicted to be 25% higher (figures 2*c* and 3). This pattern occurs because high-resource supply and increased temperature minimized juvenile mortality and optimized development rate. These effects allowed faster recruitment at 32°C, leading to increased

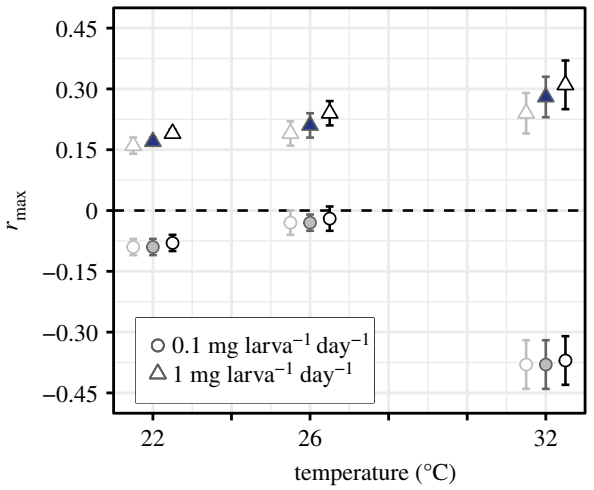

Figure 3. Population-level *Ae. aegypti* fitness (r_{max}) by resource supply (0.1 (low) or 1 mg larva^{-1} day^{-1} (high)) across temperatures. Fitness estimates for each treatment, with 95% confidence intervals (CIs). The three data points for each treatment represent r_{max} estimated using the 95% CI bounds of the exponents for the scaling of lifetime fecundity with wing length (electronic supplementary material, equation S1, figure S2). The lightest greyscale hue estimates derive from the lower 95% CIs, the mid-range hue estimates with closed symbols derive from the slopes, and the darkest hue derives from the upper 95% CIs.

fitness as greater numbers of individuals could contribute to population growth through reproductive output sooner than for other treatments. This result is consistent with empirical and theoretical studies of ectotherm fitness [60–63], including mosquitoes [32]. This finding is key, as it implies that predictions about the effect of warming on vector abundance and disease transmission based on laboratory-derived trait data (which are generally from populations under high- or optimal resource supply) likely underestimate the effect of temperature on development time and juvenile survival, and overestimate effects of temperature on lifespan and fecundity.

Indeed, the trait-level responses of our high-resource supply treatments correspond with studies that have synthesized laboratory-derived high-resource supply trait responses to temperature to estimate vector fitness and R_0. In these studies, juvenile survival is expected to be approximately 80% at 22 and 26°C and approximately 70% at 32°C [8]. In the present study, juvenile survival at high-resource supply was predicted to follow a similar pattern (approx. 80% at 22 and 26°C, and 64% at 32°C; figure 1). By contrast, juvenile survival at low-resource supply in the present study was predicted to be 65% at 22°C, 80% at 26°C and 32% at 32°C (figure 1).

Further, the juvenile development rate of most mosquito vectors is expected to increase from approximately 0.07 day^{-1} at 22°C to approximately 0.14 day^{-1} at 32°C [8], which is congruent with the present study's development rate (1/development time, figure 2*a*) at high-resource supply (approx. 0.08 to approx. 0.17 day^{-1}) across the same temperature range. By contrast, at low-resource supply, we found juvenile development rate was approximately 0.05 day^{-1} at 32°C (figure 2*a*), which is consistent with other studies on the effects of temperature and low-resource supply on juvenile development rate [38]. Such differences in juvenile trait responses are likely to substantially alter predictions about the temperature dependence of R_0. This underlines the importance of considering resource supply when predicting the temperature dependence of R_0 for vector-borne diseases.

Juvenile survival decreased significantly with temperature and was overall significantly lower at low-resource supply (figure 1). This reduction in survival is likely because somatic maintenance costs increase with metabolic rate [22], which cannot be met below a threshold resource supply level. Such metabolic costs could explain why the highest level of mortality occurred at 32°C at low-resource supply, where the energy supply-demand deficit was expected to be the largest.

The Gompertz-shaped juvenile survival curves observed at 22 and 26°C at low-resource supply (figure 1*a*) may well arise from the amount of resource being sufficient for somatic maintenance, but not for development. This hypothesis 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 and other arthropods. 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 [64] and/or the risk of exposure to breeding habitat evaporation [65]. If resource availability increases with climatic warming, the negative effects of predation and breeding habitat evaporation on population growth could be offset by increased development and recruitment rates [66]. Alternatively, population growth could be dampened, if climate change reduces the quantity of food available to ectotherms [67,68]. This effect could simultaneously decrease the burden of vector-borne diseases and agricultural pests, but increase the extinction risk of vulnerable species [69,70].

We did not measure the effect of temperature and resource supply on fecundity directly, but used the size-scaling of this trait to estimate this effect. This approach is appropriate because most of the effect of resource limitation on juveniles is expected to affect adult mosquitoes indirectly by reducing size at emergence and lifespan [30,50]. Predicted fecundity increased with temperature, with a larger increase from 26°C to 32°C than between 22°C and 26°C (figure 2*d*; electronic supplementary material, table S2). Across both resource levels, these fecundity estimates are similar to datasets that are used to parameterize mosquito-borne disease transmission models (e.g. [71]). 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 (figure 3; electronic supplementary material, figure S3).

While the increased negative carry over effects of temperature at resource limitation on adult traits had a relatively weak impact on fitness compared to juvenile traits, temperature × resource supply interactions may have important effects on other components of vector-borne disease transmission [72]. For example, larger individuals may have greater transmission potential because they are more likely to outlive a pathogen's extrinsic incubation period [73]. However, the interactive effects of temperature and resource availability can alter the relationships between body size, longevity and vector competence [74,75]. Indeed, as we have shown here, resource limitation can exaggerate the negative relationship between

size and temperature [26]. This effect could increase transmission probability as smaller *Ae. aegypti* may compensate for poor larval nutrition by biting more frequently [76]. Also, larval nutrition [37] and temperature [77] can independently influence within-vector parasite development, but future studies could consider how the combined effects of temperature and resource supply affect this, and other important transmission traits.

Another important implication of this study's findings for vector-borne disease research is that it underlines the need to develop realistic and tractable methods of measuring density-dependent effects on population fitness in the field. Without such datasets, it will not be possible to link temperature- and resource-dependent fitness to vector abundance dynamics and VBD dynamics. Semi-field systems offer a way to track the entire mosquito life cycle under ambient environmental conditions [78]. Such systems are generally being used to test the effectiveness of novel biocontrol strategies, such as transgenic fungi [79], but they also could allow for the effects of temperature × resource interactions on fitness and abundance to be explored under conditions that more closely resemble natural environments. State of the art insect traps and geospatial mapping of microclimates and vegetation indices could also be used to study the effects of variation in temperature and resource availability on vector populations in the field [80,81].

In this study, we did not consider 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 relationship occurs because microbial growth rates increase with temperature to some optimum, which may increase the concentration of food in the environment [9,82,83]. For example, *Anopheles* [84] and *Aedes* [85] mosquitoes can be reared exclusively on cultures of *Asaia* bacteria. We also did not address larval competition for resources by manipulating the number of larvae for a given resource supply level. Variation in larval density may introduce additional fitness constraints through interference and exploitative competition. It could also interact with temperature-dependent resource supply because a higher larval density will increase accumulation of waste products. These are interesting and potentially important avenues for future investigation.

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 availability between the radically different temperature responses as we have found here (figure 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 [18–20,86]. Our study underlines the importance of the effects of resource supply on the temperature dependence of population-level fitness of an important disease vector. In doing so, our findings suggest that current projections of how climatic warming affects vector-borne disease transmission may prove inaccurate because they generally fail to consider resource limitations. Our findings also underline the need for a future research effort to be directed at better understanding how temperature and resource supply interact in the field, and how this, and interactions between other environmental factors, may influence other components of vector-borne disease systems. While recent studies have shown that interactions between temperature and resource availability can have important effects on population fitness in single-celled organisms [21,58,59], our results show that such interactions also need to be considered when predicting how eukaryotes will respond to environmental change.

Data accessibility. All data for analyses are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.h9w0vt4gg [88]. A preprint version of this manuscript is available from the bioRxiv preprint server: https://doi.org/10.1101/2020.05.29.123315 [89].

Authors' contributions. All authors contributed to the conception of the study and designed the experiments, L.J.C. provided the mosquitoes; P.J.H. and S.P. performed the modelling; P.J.H. collected the data and analysed it. P.J.H. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Competing interests. We declare we have no competing interests.

Funding. This study was supported by Natural Environment Research Council (NE/L002515/1). We also acknowledge joint Centre funding from the UK Medical Research Council and Department for International Development (MR/R0156600/1).

References

1. Stanaway JD *et al.* 2016 The global burden of dengue: an analysis from the Global Burden of Disease Study 2013. *Lancet Infect. Dis.* **16**, 712–723. (doi:10.1016/S1473-3099(16)00026-8)
2. World Health Organization. 2014 A global brief on vector-borne diseases. *World Heal. Organ.* WHO/DCO/WHD/2014. **1**, 1–56.
3. Li R, Xu L, Bjørnstad ON, Liu K, Song T, Chen A, Xu B, Liu Q, Stenseth NC. 2019 Climate-driven variation in mosquito density predicts the spatiotemporal dynamics of dengue. *Proc. Natl Acad. Sci.* **116**, 3624–3629. (doi:10.1073/pnas.1806094116)
4. Ng K-C, Chaves L, Tsai K-H, Chuang T-W. 2018 Increased adult *Aedes aegypti* and *Culex quinquefasciatus* (Diptera: Culicidae) abundance in a dengue transmission hotspot, compared to a coldspot, within Kaohsiung City, Taiwan. *Insects* **9**, 98. (doi:10.3390/insects9030098)
5. Mordecai EA, Ryan SJ, Caldwell JM, Shah MM, LaBeaud AD. 2020 Climate change could shift disease burden from malaria to arboviruses in Africa. *Lancet Planet. Health* **4**, e416–e423. (doi:10.1016/S2542-5196(20)30178-9)
6. Ryan SJ, Carlson CJ, Tesla B, Bonds MH, Ngonghala CN, Mordecai EA, Johnson LR, Murdock CC. 2021 Warming temperatures could expose more than 1.3 billion new people to Zika virus risk by 2050. *Glob. Chang. Biol.* **27**, 84–93. (doi:10.1111/gcb.15384)
7. Cator LJ *et al.* 2020 The role of vector trait variation in vector-borne disease dynamics. *Front. Ecol. Evol.* **8**, 1–25. (doi:10.3389/fevo.2020.00189)
8. Mordecai EA *et al.* 2019 Thermal biology of mosquito-borne disease. *Ecol. Lett.* **22**, 1690–1708. (doi:10.1111/ele.13335)

9. Cross WF, Hood JM, Benstead JP, Huryn AD, Nelson D. 2015 Interactions between temperature and nutrients across levels of ecological organization. *Glob. Chang. Biol.* **21**, 1025–1040. (doi:10.1111/gcb.12809)
10. Iwamura T, Guzman-Holst A, Murray KA. 2020 Accelerating invasion potential of disease vector *Aedes aegypti* under climate change. *Nat. Commun.* **11**, 2130. (doi:10.1038/s41467-020-16010-4)
11. Parham PE, Michael E. 2010 Modeling the effects of weather and climate change on malaria transmission. *Environ. Health Perspect.* **118**, 620–626. (doi:10.1289/ehp.0901256)
12. Liu-Helmersson J, Stenlund H, Wilder-Smith A, Rocklö J. 2014 Vectorial capacity of *Aedes aegypti*: effects of temperature and implications for global dengue epidemic potential. *PLoS ONE* **9**, e89783. (doi:10.1371/journal.pone.0089783)
13. Miazgowicz KL *et al.* 2020 Age influences the thermal suitability of *Plasmodium falciparum* transmission in the Asian malaria vector *Anopheles stephensi*. *Proc. R. Soc. B* **287**, 20201093. (doi:10.1098/rspb.2020.1093)
14. Shocket MS, Verwillow AB, Numazu MG, Slamani H, Cohen JM, El Moustaid F, Rohr J, Johnson LR, Mordecai EA. 2020 Transmission of West Nile and five other temperate mosquito-borne viruses peaks at temperatures between 23°C and 26°C. *Elife* **9**, 1–67. (doi:10.7554/eLife.58511)
15. Hamlet A, Jean K, Perea W, Yactayo S, Biey J, Van Kerkhove M, Ferguson N, Garske T. 2018 The seasonal influence of climate and environment on yellow fever transmission across Africa. *PLoS Negl. Trop. Dis.* **12**, e0006284. (doi:10.1371/journal.pntd.0006284)
16. Dell AI, Pawar S, Savage VM. 2011 Systematic variation in the temperature dependence of physiological and ecological traits. *Proc. Natl Acad. Sci.* **108**, 10 591–10 596. (doi:10.1073/pnas.1015178108)
17. Mordecai EA *et al.* 2013 Optimal temperature for malaria transmission is dramatically lower than previously predicted. *Ecol. Lett.* **16**, 22–30. (doi:10.1111/ele.12015)
18. Arrivillaga J, Barrera R. 2004 Food as a limiting factor for *Aedes aegypti* in water-storage containers. *J. Vector Ecol.* **29**, 11–20.
19. Barrera R, Amador M, Clark GG. 2006 Ecological factors influencing *Aedes aegypti* (Diptera: Culicidae) productivity in artificial containers in Salinas, Puerto Rico. *J. Med. Entomol.* **43**, 484–492. (doi:10.1093/jmedent/43.3.484)
20. Walsh RK, Facchinelli L, Ramsey JM, Bond JG, Gould F. 2011 Assessing the impact of density dependence in field populations of *Aedes aegypti*. *J. Vector Ecol.* **36**, 300–307. (doi:10.1111/j.1948-7134.2011.00170.x)
21. Thomas MK, Aranguren-Gassis M, Kremer CT, Gould MR, Anderson K, Klausmeier CA, Litchman E. 2017 Temperature-nutrient interactions exacerbate sensitivity to warming in phytoplankton. *Glob. Chang. Biol. March.* **23**, 3269–3280. (doi:10.1111/gcb.13641)
22. Kooijman SALM. 2000 *Dynamic energy and mass budgets in biological systems*. Cambridge, UK: Cambridge University Press.
23. West GB, Brown JH, Enquist BJ. 2001 A general model for ontogenetic growth. *Nature* **413**, 628–631. (doi:10.1038/35098076)
24. Savage VM, Gillooly JF, Brown JH, West GB, Charnov EL. 2004 Effects of body size and temperature on population growth. *Am. Nat.* **163**, 429–441. (doi:10.1086/381872)
25. Amarasekare P, Savage V. 2012 A framework for elucidating the temperature dependence of fitness. *Am. Nat.* **179**, 178–191. (doi:10.1086/663677)
26. Atkinson D. 1994 Temperature and organism size—a biological law for ectotherms? *Adv. Ecol. Res.* **25**, 1–58. (doi:10.1016/S0065-2504(08)60212-3)
27. Rueda LM, Patel KJ, Axtell RC, Stinner RE. 1990 Temperature-dependent development and survival rates of *Culex quinquefasciatus* and *Aedes aegypti* (Diptera: Culicidae). *J. Med. Entomol.* **27**, 892–898. (doi:10.1093/jmedent/27.5.892)
28. Forster J, Hirst AG, Atkinson D. 2012 Warming-induced reductions in body size are greater in aquatic than terrestrial species. *Proc. Natl Acad. Sci. USA* **109**, 19 310–19 314. (doi:10.1073/pnas.1210460109)
29. Nasci RS. 1991 Influence of larval and adult nutrition on biting persistence in *Aedes aegypti* (Diptera: Culicidae). *J. Med. Entomol.* **28**, 522–526. (doi:10.1093/jmedent/28.4.522)
30. Steinwascher K. 1982 Relationship between pupal mass and adult survivorship and fecundity for *Aedes aegypti*. *Environ. Entomol.* **11**, 150–153. (doi:10.1093/ee/11.1.150)
31. Brady OJ, Hay SI. 2020 The global expansion of dengue: how *Aedes aegypti* mosquitoes enabled the first pandemic arbovirus. *Annu. Rev. Entomol.* **65**, 191–208. (doi:10.1146/annurev-ento-011019-024918)
32. Dye C. 1984 Models for the population dynamics of the yellow fever mosquito, *Aedes aegypti*. *J. Anim. Ecol.* **53**, 247. (doi:10.2307/4355)
33. Gilpin ME, McClelland GA. 1979 Systems analysis of the yellow fever mosquito *Aedes aegypti*. *Fortschr. Zool.* **25**, 355–388.
34. Walsh RK, Aguilar CL, Facchinelli L, Valerio L, Ramsey JM, Scott TW, Lloyd AL, Gould F. 2013 Regulation of *Aedes aegypti* population dynamics in field systems: quantifying direct and delayed density dependence. *Am. J. Trop. Med. Hyg.* **89**, 68–77. (doi:10.4269/ajtmh.12-0378)
35. Gimnig JE, Ombok M, Otieno S, Kaufman MG, Vulule JM, Walker ED. 2002 Density-dependent development of *Anopheles gambiae* (Diptera: Culicidae) larvae in artificial habitats. *J. Med. Entomol.* **39**, 162–172. (doi:10.1603/0022-2585-39.1.162)
36. Romeo Aznar V, Alem I, De Majo MS, Byttebier B, Solari HG, Fischer S. 2018 Effects of scarcity and excess of larval food on life history traits of *Aedes aegypti* (Diptera: Culicidae). *J. Vector Ecol.* **43**, 117–124. (doi:10.1111/jvec.12291)
37. Shapiro LLM, Murdock CC, Jacobs GR, Thomas RJ, Thomas MB. 2016 Larval food quantity affects the capacity of adult mosquitoes to transmit human malaria. *Proc. R. Soc. B* **283**, 20160298. (doi:10.1098/rspb.2016.0298)
38. Couret J, Dotson E, Benedict MQ. 2014 Temperature, larval diet, and density effects on development rate and survival of *Aedes aegypti* (Diptera: Culicidae). *PLoS ONE* **9**, 1–9. (doi:10.1371/journal.pone.0087468)
39. Padmanabha H, Correa F, Legros M, Nijhout HF, Lord C, Lounibos LP. 2012 An eco-physiological model of the impact of temperature on *Aedes aegypti* life history traits. *J. Insect Physiol.* **58**, 1597–1608. (doi:10.1016/j.jinsphys.2012.09.015)
40. Arguez A, Durre I, Applequist S, Vose RS, Squires MF, Yin X, Heim RR, Owen TW. 2012 NOAA's 1981–2010U.S. Climate normals: an overview. *Bull. Am. Meteorol. Soc.* **93**, 1687–1697. (doi:10.1175/BAMS-D-11-00197.1)
41. Bargielowski IE, Lounibos LP, Carrasquilla MC. 2013 Evolution of resistance to satyrization through reproductive character displacement in populations of invasive dengue vectors. *Proc. Natl Acad. Sci. USA* **110**, 2888–2892. (doi:10.1073/pnas.1219599110)
42. Farjana T, Tuno N. 2012 Effect of body size on multiple blood feeding and egg retention of *Aedes aegypti* (L.) and *Aedes albopictus* (Skuse) (Diptera: Culicidae). *Med. Entomol. Zool.* **63**, 123–131. (doi:10.7601/mez.63.123)
43. Caswell H. 1989 *Matrix population models construction, analysis, and interpretation*. Sunderland, MA: Sinauer Associates.
44. Birch LC. 1948 The intrinsic rate of natural increase of an insect population. *J. Anim. Ecol.* **17**, 15. (doi:10.2307/1605)
45. Cole LC. 1954 The population consequences of life history phenomena. *Q. Rev. Biol.* **29**, 103–137. (doi:10.1086/400074)
46. R Core Team. 2018 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See http://www.R-project.org/.
47. Stubben C, Milligan B. 2007 Estimating and analyzing demographic models using the popbio package in R. *J. Stat. Softw.* **22**, 1–23. (doi:10.18637/jss.v022.i11)
48. Therneau T. 2021 A package for survival analysis in R. R package version 3.2-10. See https://CRAN.R-project.org/package=survival.
49. Agnew P, Hide M, Sidobre C, Michalakis Y. 2002 A minimalist approach to the effects of density-dependent competition on insect life-history traits. *Ecol. Entomol.* **27**, 396–402. (doi:10.1046/j.1365-2311.2002.00430.x)
50. Briegel H. 1990 Metabolic relationship between female body size, reserves, and fecundity of *Aedes aegypti*. *J. Insect Physiol.* **36**, 165–172. (doi:10.1016/0022-1910(90)90118-Y)
51. Focks DA, Haile D, Daniels E, Mount GA. 1993 Dynamic life table model for *Aedes aegypti* (Diptera:

Culicidae): simulation results and validation. *J. Med. Entomol.* **30**, 1018–1028. (doi:10.1093/jmedent/30.6.1018)

52. Juliano SA. 1998 Species introduction and replacement among mosquitoes: interspecific resource competition or apparent competition? *Ecology* **79**, 255. (doi:10.2307/176880)
53. Skalski JR, Millspaugh JJ, Dillingham P, Buchanan RA. 2007 Calculating the variance of the finite rate of population change from a matrix model in Mathematica. *Environ. Model. Softw.* **22**, 359–364. (doi:10.1016/j.envsoft.2005.12.003)
54. Hope RM. 2013 Rmisc: Rmisc: Ryan Miscellaneous. See https://CRAN.R-project.org/package=Rmisc.
55. Caswell H, Naiman RJ, Morin R. 1984 Evaluating the consequences of reproduction in complex salmonid life cycles. *Aquaculture* **43**, 123–134. (doi:10.1016/0044-8486(84)90016-4)
56. de Kroon H, Plaisier A, van Groenendael J, Caswell H. 1986 Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* **67**, 1427–1431. (doi:10.2307/1938700)
57. Jackson C. 2016 flexsurv: a platform for parametric survival modeling in R. *J. Stat. Softw.* **70**, 1–33. (doi:10.18637/jss.v070.i08)
58. Bestion E, Schaum C-E, Yvon-Durocher G. 2018 Nutrient limitation constrains thermal tolerance in freshwater phytoplankton. *Limnol. Oceanogr. Lett.* **3**, 436–443. (doi:10.1002/lol2.10096)
59. Hall E, Cotner J. 2007 Interactive effect of temperature and resources on carbon cycling by freshwater bacterioplankton communities. *Aquat. Microb. Ecol.* **49**, 35–45. (doi:10.3354/ame01124)
60. Huey RB, Berrigan D. 2001 Temperature, demography, and ectotherm fitness. *Am. Nat.* **158**, 204–210. (doi:10.1086/321314)
61. Caswell H. 1978 A general formula for the sensitivity of population growth rate to changes in life history parameters. *Theor. Popul. Biol.* **14**, 215–230. (doi:10.1016/0040-5809(78)90025-4)
62. Kammenga JE, Busschers M, Van Straalen NM, Jepson PC, Bakker J. 1996 Stress induced fitness reduction is not determined by the most sensitive life-cycle trait. *Funct. Ecol.* **10**, 106. (doi:10.2307/2390268)
63. Forbes VE, Olsen M, Palmqvist A, Calow P. 2010 Environmentally sensitive life-cycle traits have low elasticity: implications for theory and practice. *Ecol. Appl.* **20**, 1449–1455. (doi:10.1890/09-1063.1)
64. Benrey B, Denno RF. 1997 The slow-growth–high-mortality hypothesis: a test using the cabbage butterfly. *Ecology* **78**, 987. (doi:10.2307/2265852)
65. Fillinger U, Sonye G, Killeen GF, Knols BGJ, Becker N. 2004 The practical importance of permanent and semipermanent habitats for controlling aquatic stages of *Anopheles gambiae* sensu lato mosquitoes: operational observations from a rural town in western Kenya. *Trop. Med. Int. Heal.* **9**, 1274–1289. (doi:10.1111/j.1365-3156.2004.01335.x)
66. Culler LE, Ayres MP, Virginia RA. 2015 In a warmer Arctic, mosquitoes avoid increased mortality from predators by growing faster. *Proc. R. Soc. B* **282**, 20151549. (doi:10.1098/rspb.2015.1549)
67. Lister BC, Garcia A. 2018 Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proc. Natl Acad. Sci.* **115**, E10397–E10406. (doi:10.1073/pnas.1722477115)
68. Huey RB, Kingsolver JG. 2019 Climate warming, resource availability, and the metabolic meltdown of ectotherms. *Am. Nat.* **194**, E140–E150. (doi:10.1086/705679)
69. Wagner DL, Grames EM, Forister ML, Berenbaum MR, Stopak D. 2021 Insect decline in the Anthropocene: death by a thousand cuts. *Proc. Natl Acad. Sci.* **118**, e2023989118. (doi:10.1073/pnas.2023989118)
70. Lehmann P *et al.* 2020 Complex responses of global insect pests to climate warming. *Front. Ecol. Environ.* **18**, 141–150. (doi:10.1002/fee.2160)
71. Yang HM, Macoris MLG, Galvani KC, Andrighetti MTM, Wanderley DMV. 2009 Assessing the effects of temperature on the population of *Aedes aegypti*, the vector of dengue. *Epidemiol. Infect.* **137**, 1188–1202. (doi:10.1017/S0950268809002040)
72. Parham PE *et al.* 2015 Climate, environmental and socio-economic change: weighing up the balance in vector-borne disease transmission. *Phil. Trans. R. Soc. B* **370**, 20130551. (doi:10.1098/rstb.2013.0551)
73. Bellan SE. 2010 The importance of age dependent mortality and the extrinsic incubation period in models of mosquito-borne disease transmission and control. *PLoS ONE* **5**, e10165. (doi:10.1371/journal.pone.0010165)
74. Barreaux AMG, Stone CM, Barreaux P, Koella JC. 2018 The relationship between size and longevity of the malaria vector *Anopheles gambiae* (s.s.) depends on the larval environment. *Parasit. Vectors* **11**, 485. (doi:10.1186/s13071-018-3058-3)
75. Barreaux AMG, Barreaux P, Thievent K, Koella JC. 2016 Larval environment influences vector competence of the malaria mosquito *Anopheles gambiae*. *MalariaWorld J.* **7**, 1–6. (doi:10.1186/s13071-018-3058-3)
76. Scott TW, Morrison AC, Lorenz LH, Clark GG, Strickman D, Kittayapong P, Zhou H, Edman JD. 2000 Longitudinal studies of *Aedes aegypti* (Diptera: Culicidae) in Thailand and Puerto Rico: population dynamics. *J. Med. Entomol.* **37**, 77–88. (doi:10.1603/0022-2585-37.1.77)
77. Shapiro LLM, Whitehead SA, Thomas MB. 2017 Quantifying the effects of temperature on mosquito and parasite traits that determine the transmission potential of human malaria. *PLoS Biol.* **15**, e2003489. (doi:10.1371/journal.pbio.2003489)
78. Jones RT, Ant TH, Cameron MM, Logan JG. 2021 Novel control strategies for mosquito-borne diseases. *Phil. Trans. R. Soc. B* **376**, 20190802. (doi:10.1098/rstb.2019.0802)
79. Lovett B, Bilgo E, Millogo SA, Ouattarra AK, Sare I, Gnambani EJ, Dabire RK, Diabate A, St. Leger RJ. 2019 Transgenic *Metarhizium* rapidly kills mosquitoes in a malaria-endemic region of Burkina Faso. *Science* **364**, 894–897. (doi:10.1126/science.aaw8737)
80. Wimberly MC, Davis JK, Evans MV, Hess A, Newberry PM, Solano-Asamoah N, Murdock CC. 2020 Land cover affects microclimate and temperature suitability for arbovirus transmission in an urban landscape. *PLoS Negl. Trop. Dis.* **14**, e0008614. (doi:10.1371/journal.pntd.0008614)
81. Høye TT *et al.* 2021 Deep learning and computer vision will transform entomology. *Proc. Natl Acad. Sci.* **118**, e2002545117. (doi:10.1073/pnas.2002545117)
82. Craine JM, Fierer N, McLauchlan KK. 2010 Widespread coupling between the rate and temperature sensitivity of organic matter decay. *Nat. Geosci.* **3**, 854–857. (doi:10.1038/ngeo1009)
83. Smith TP, Thomas TJH, García-Carreras B, Sal S, Yvon-Durocher G, Bell T, Pawar S. 2019 Community-level respiration of prokaryotic microbes may rise with global warming. *Nat. Commun.* **10**, 5124. (doi:10.1038/s41467-019-13109-1)
84. Chouaia B *et al.* 2012 Delayed larval development in *Anopheles* mosquitoes deprived of *Asaia* bacterial symbionts. *BMC Microbiol.* **12**, S2. (doi:10.1186/1471-2180-12-S1-S2)
85. Souza RS, Virginio F, Riback TIS, Suesdek L, Barufi JB, Genta FA. 2019 Microorganism-based larval diets affect mosquito development, size and nutritional reserves in the yellow fever mosquito *Aedes aegypti* (Diptera: Culicidae). *Front. Physiol.* **10**, 1–24. (doi:10.3389/fphys.2019.00152)
86. Subra R, Mouchet J. 1984 The regulation of preimaginal populations of *Aedes aegypti* (L.) (Diptera: Culicidae) on the Kenya coast. *Ann. Trop. Med. Parasitol.* **78**, 63–70. (doi:10.1080/00034983.1984.11811774)
87. Orcutt JD, Porter KG. 1984 The synergistic effects of temperature and food concentration of life history parameters of *Daphnia*. *Oecologia* **63**, 300–306. (doi:10.1007/BF00390657)
88. Huxley PJ, Murray KA, Pawar S, Cator LJ. 2021 Data from: The effect of resource limitation on the temperature dependence of mosquito population fitness. Dryad Digital Repository. (https://doi.org/10.5061/dryad.h9w0vt4gg)
89. Huxley PJ, Murray KA, Pawar S, Cator LJ. 2020 The effect of resource limitation on the temperature-dependence of mosquito population fitness. *bioRxiv* 1–15. (doi:10.1101/2020.05.29.123315)