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Title: Competition in depleting resource environments shapes the thermal response of mosquito population fitness

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

[1]MRC Centre for Global Infectious Disease Analysis, Department of Infectious Disease Epidemiology, 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.

Correspondence should be sent to:

Paul J. Huxley

MRC Centre for Global Infectious Disease Analysis
Department of Infectious Disease Epidemiology
Imperial College London
Norfolk Place, London
W2 1PG
p.huxley@imperial.ac.uk

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ABSTRACT

1. A population's maximal growth rate (r_m) depends on the survivorship, development, and reproduction of its individuals. In ectotherms, these (functional) traits respond predictably to temperature, which provides a basis for predicting how climatic warming could affect natural populations, including disease vectors and the diseases they transmit.
2. Such predictions generally arise from mathematical models that incorporate the temperature-dependence of traits (thermal performance curves) measured under laboratory conditions. Therefore, the accuracy of these predictions depends on the relevance of lab-measured trait thermal performance curves to natural conditions. However, the joint effect of temperature and resource availability—another key limiting environmental factor in nature—on traits is largely unknown.
3. We investigated how larval competition for ecologically-realistic depleting resources affects the thermal performance of r_m and its underlying life history traits in the disease vector in *Aedes aegypti*. We show that competition at food concentrations below a certain threshold drastically depresses r_m across the entire temperature range, causes it to peak at a lower temperature, and narrows the breadth of temperatures over which r_m is positive (the thermal niche breath).
4. This resource-dependence of the thermal performance curve of r_m is driven primarily by the fact that competition delays development and increases juvenile mortality. This is compounded by reduced size at maturity, which in turn decreases adult lifespan and fecundity.
5. These results show that intensified larval competition in depleting resource environments can significantly affect the temperature-dependence of r_m by modulating the thermal responses of underlying traits in a predictable way. This has important implications for forecasting the effects of climate change on population dynamics in the field of not just disease vectors, but holometabolous insects in general.

Key words: ectotherm, climatic warming, r_m, population-level fitness, thermal performance curve, resource depletion, competition, vector-borne disease.

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INTRODUCTION

Environmental change is predicted to affect the spatiotemporal distributions of ectotherms (Deutsch et al. 2008), including disease vectors (Mordecai et al. 2020, WHO 2020). For example, recent studies suggest that climatic warming may increase the thermal suitability for Zika virus transmission, leading to 1.3 billion more people being at risk of exposure by 2050 (Ryan et al. 2021). Such predictions often arise from disease transmission models that incorporate thermal performance curves (TPCs) for vector life history traits, such as juvenile development and mortality, which together define the TPC of maximal population growth rate (r_m, a measure of population fitness; Savage et al. 2004).

Typically, trait-level TPCs are obtained from data that come from vector populations reared under optimal food conditions in the laboratory. Yet, in nature insect populations experience spatiotemporal variation in resource availability. Indeed, very few empirical studies have examined how the r_m TPC may be shaped by intraspecific competition (but see Johnson et al. 2016, Mallard et al. 2020). In particular, the effect of competition for depleting resources on the r_m TPC through its effects on underlying traits has been rarely studied, although resource depletion in adult and larval habitats is arguably a common scenario in nature (Ostfeld and Keesing 2000, Wright 1983, Yee and Juliano 2012). For example, resource depletion should occur at a faster rate with rising temperatures because per capita energy requirements for somatic maintenance and growth increase with temperature (Kooijman 2000, West et al. 2001).

As competition intensifies with increasing temperature and resource depletion rates, the growth, development, and survival of increasing numbers of individuals are bound to be compromised. These trait-level effects are then expected to propagate through the stage-structured population dynamics to change the shape of the r_m TPC (Amarasekare and Savage 2012, Huey and Kingsolver 2019). This is because r_m is essentially proportional to the difference between biomass gained through consumption and that lost to respiration and mortality (Savage et al. 2004). Resource limitation and competition would be expected to decrease r_m across temperatures as they would both undermine biomass intake and elevate biomass loss. Furthermore, if the rate of biomass loss increases faster than any increase in biomass gain with temperature, the thermal optimum of r_m (T_{opt}) may also shift downwards (García-Carreras et al. 2018). For the same reason, the range of temperatures over which r_m is

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positive (the thermal niche width) may become narrower. As a result, species range boundaries could contract due to the combined effects of climatic warming and intensified competition. Conversely, concurrent increases in temperature and resource availability with climatic warming would optimise r_m, promoting the invasion of tropical taxa into temperate habitats (Amarasekare and Simon 2020).

Studies on how intraspecific larval competition affects the r_m TPC are rare, but recent empirical work provides some insights into how competition may affect fitness traits. For example, a study of the bordered plant bug suggests that intraspecific competition between adults for resources is strongest at temperatures that are optimal for reproduction (Johnson et al. 2016). Other studies suggest that the effects of competition on individual growth rates, fecundity and body size may change as the thermal environment and population dynamics change (Laws and Belovsky 2010, Mallard et al. 2020). However, despite these advances, the question of whether and how larval competition in depleting resource environments can alter the shape of the r_m TPC remains open.

Addressing this question is particularly important for semiaquatic insects, such as mosquitoes. This is because such species are expected to be mainly regulated by larval competition for limited resources (Dye 1984), and have juvenile stages that are restricted to small, ephemeral aquatic habitats that are susceptible to infrequent resource inputs (Arrivillaga and Barrera 2004, Barrera et al. 2006, Yee and Juliano 2012). Here, we investigate the effects of intraspecific competition on the r_m TPC by exposing *Ae. aegypti* larvae to a realistic range of temperatures and resource concentration levels. We show that, in this species, intensified larval competition at low resource concentration can significantly change the shape of the r_m TPC through its effects on underlying traits in a predictable and general way.

METHODS

To investigate the effects of temperature and larval competition for food on mosquito life history, we employed a 5 × 4 factorial design comprised of five temperatures (22, 26, 32, 34, and 36°C) and resource concentration levels (0.183, 0.367, 0.550 and 0.733 mg ml^{-1}). These resource levels simulate a situation where juvenile habitats do not receive any additional resource during the timescale relevant to our single generation study. Ensuring constant

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resource concentration was important to isolate the effects of competition in depleting resource environments. The experiment was carried out in two consecutive blocks. Temperatures were randomly selected to determine the order in which they were to be tested. The first block comprised of 22, 34 and 36°C, the second comprised of 26 and 32°C. We selected our temperature range to span the minimum and maximum temperatures (approximately 22 to 34°C) that this strain of *Ae. aegypti* is likely to experience in the wild between May (the onset of mosquito season) and November (Fort Meyer, FL; Arguez et al. 2012). We extended our range to 36°C to determine the upper critical thermal limit for this strain.

Batches of approximately 800 *Ae. aegypti* (F16-19) eggs were randomly assigned to one of the five experimental temperatures and immersed in plastic tubs containing 300 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, 32, 34, or 36°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 50 and held in tubs containing 300 ml of water. We created three replicate tubs per treatment (150 individuals treatment^{-1}). Resource concentration levels were attained by adding 55, 110 and 220 mg to the tubs, respectively. Prior testing of these levels resulted in high levels of juvenile mortality due to fouling at the higher temperature × resource levels. Therefore, for all treatments, half of the assigned food quantity was provided on Day 1. The remaining half was provided on Day 4 after any remaining food from Day 1 had been sieved and rearing waters had been replenished with fresh tap water. After Day 4, resource levels were not adjusted but water volumes were adjusted, as required.

Fitness calculation

To calculate r_m, we used our life history trait data to parameterise stage-structured matrix projection models (eqn. 1; Caswell 1989), which describe change in a population over time:

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$$\mathbf{N}_{t+1} = \mathbf{M}\mathbf{N}_t, \quad (1)$$

where $\mathbf{N}_t$ is a vector of abundances in the stage classes at time t and **M** is the population projection matrix. The first row of **M** is populated by daily fecundity (the number of female offspring produced per female at age i). The sub-diagonal of **M** is populated with the probabilities of survival from age i to age i+1. Multiplying the transition matrix (**M**; eqn. 1) and stage-structured population size vector ($\mathbf{N}_t$; eqn. 1) 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) (Caswell 1989). Then, the intrinsic rate of population growth is

$$r_{\mathrm{m}} = \log(\lambda).$$

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

Model parameterisation

Immature development time and immature and adult survival proportions

Matrix survival elements (the sub-diagonal of the matrix **M**; eqn. 1) were populated with continuous survival proportions estimated using the Kaplan-Meier survival function in the `survival` R package (R Core Team 2018, Therneau 2020). 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. Adult lifespan was recorded in the absence of food, which forces adults to metabolise the nutritional reserves accumulated during larval development. Therefore, starved adult lifespan should increase with size at emergence, so it is a useful indicator of the carry over effects of temperature and competition in the larval habitat (Agnew et al. 2002, Briegel 1990).

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Daily fecundity rate

The use of scaling relationships between fecundity and size is common in predictions of population growth in *Aedes* mosquitoes (Focks et al. 1993, Juliano 1998). A detailed description of our method for estimating fecundity is provided in the supplementary material (Fig. S1). Briefly, we measured individual dry mass, and estimated lifetime fecundity using previously published datasets on the temperature-dependent scaling between mass and wing length (van den Heuvel 1963), and wing length and fecundity (Briegel 1990, Farjana and Tuno 2012). Daily fecundity rate is required for the matrix projection models (eqn. 1), so we divided lifetime fecundity by lifespan and multiplied by 0.5 (assuming a 1:1 male-to-female offspring ratio) to give temperature-specific individual daily fecundity. Later, we show that this much variation in the scaling of fecundity does not qualitatively change our results.

Parameter sensitivity

We used the delta method to approximate 95% confidence intervals (CIs) to account for how uncertainty in survival and fecundity estimates is propagated through to the r_m estimate (Caswell 1989, Skalski et al. 2007). 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 (Table S2) for each treatment using the `Rmisc` R package (Hope 2013). As an additional sensitivity analysis, we recalculated fitness using the upper and lower 95% CIs of the exponents for the scaling of size and lifetime fecundity (Fig. S3).

Elasticity analysis

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

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calculated using the relationship: $e_{ij} = a_{ij}/\lambda \times s_{ij}$. Multiplying an elasticity by λ gives the absolute contribution of its corresponding a_{ij} to λ (Caswell et al. 1984, de Kroon et al. 1986). Absolute contributions for juvenile and adult elements were summed and changed proportionally to quantify the sensitivity of r_m to these traits.

Statistical analyses

All statistical analyses were conducted using R (R Core Team 2018). The trait data (adult lifespan and body size) were normally distributed, so we used full factorial linear models (LM) to determine the significance of each predictor on the thermal response of each of these traits. The development time data were nonlinear, positive, and right skewed, so we used a generalized linear model (GLM) with gamma distribution and identity link functions (predictor effects were considered additive). Replicate was included in all regression models as a fixed effect. We investigated the effect of larval competition on the temperature-dependency of daily per capita juvenile mortality rate by fitting an exponential function to the survival data with R package `flexsurv` (Jackson 2016). The final mortality model was obtained by dropping terms from the full model (consisting of temperature × resource level + 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).

Quantifying r_m's thermal performance curve

To determine how competition affected the shape of the r_m TPC, we fitted several mathematical models that allow for negative values at both cold and hot extremes, including polynomial models using linear regression, as well as non-linear models with non-linear least squares (NLLS) using the `rTPC` R package (Padfield et al. 2020). Overall, the Lactin2 (Lactin et al. 1995) and Kamykowski (Kamykowski and McCollum 1986) models were equally best-fitting according to the Akaike Information Criterion (AIC) (Table S4). From these, we picked the Kamykowski model because it was better at describing the estimated r_m at our lowest resource level. This model is defined as

$$r_m(T) = a(1-e^{-b(T-T_{min})})(1-e^{-c(T_{max}-T)}),$$

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where T (°C), and T_{max} and T_{min} are the high and low temperatures at which r_m becomes negative, respectively, and a, b, and c, are shape parameters without any biological meaning. Bootstrapping was used to calculate 95% prediction bounds for each r_m TPC (Padfield et al. 2020) and confidence intervals (CIs) around its T_{opt}, as well as the thermal niche width (T_{max} – T_{min}).

RESULTS

All trait responses varied significantly with temperature and resource level, with a significant interaction between the two environmental variables (Fig. 1, Tables S1, S2). Therefore, the realised effect of temperature on trait responses was consistently and significantly mediated by the how the depletion of resources at low resource availability increased the negative effects of intraspecific competition.

Competition at low resource concentration (0.183 mg ml^{-1}) increased the negative effect of increased temperature on juvenile mortality rate (Fig. 1a, Table S2). As temperatures increased from 22 to 34°C, non-overlapping 95% credible intervals indicate that juvenile mortality rate was significantly higher at low resource concentration than at the intermediate resource concentration (0.367 mg ml^{-1}). At 0.183 mg ml^{-1}, it increased from 0.05 at 22°C to 0.14 individual^{-1} day^{-1} at 34°C, whereas, at 0.367 mg ml^{-1}, it increased from 0.04 to 0.05 individual^{-1} day^{-1} across this temperature range.

Development time varied significantly with the interaction between temperature and resource concentration (ANOVA; $F_{9,\ 2.24}$ = 13.44, p<0.001, Table S1). Development time decreased with temperature at all resource levels, but the decrease with temperature was greater at the low resource level than at higher resource levels due to intensified competition. At 0.183 mg ml^{-1}, development time decreased from 18.30 days at 22°C to 8.26 days at 34°C. Development time at the higher resource levels decreased from approximately 13.50 days at 22°C to ~7.50 days at 34°C (Table S2).

Intensified competition at low resource concentration resulted in significant variation in size at maturity (mass, mg) between resource levels (ANOVA; $F_{9,0.92}$ = 24.26, p<0.001, Table S1). Adult size decreased both at warmer temperatures and at lower food concentration, though the decrease with temperature was greater at higher resource levels than at the low

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resource level. At low resource concentration, size decreased by 0.13 mg as temperatures increased from 22 to 34°C, while at the highest resource concentration (0.733 mg ml^{-1}), size decreased by 0.26 mg (Fig 1c, Table S2).

Adult lifespan varied significantly with the interaction between temperature and resource concentration (ANOVA; $F_{9, 699.60} = 7.96$, $p<0.001$, Table S1). Lifespan was greatest at 0.733 mg ml^{-1}, where it was 11.24 days at 22°C. It increased to 11.65 days at 26°C, and then decreased to 4.68 days at 34°C. In contrast, at low resource concentration, lifespan decreased from 8.00 days at 22°C to 3.76 days at 34°C mg (Fig 1d, Table S2).

At all resource levels, predicted daily fecundity rate increased with temperature (Table S2), though the increase was greater at low resource concentration than at higher resource levels. At low resource concentration, fecundity increased with temperature from 1.77 eggs $individual^{-1}$ day^{-1} at 22°C to 6.87 eggs $individual^{-1}$ day^{-1} at 34°C. At the higher resource levels, fecundity increased from ~2 eggs at 22°C to ~5 eggs $individual^{-1}$ day^{-1} at 34°C.

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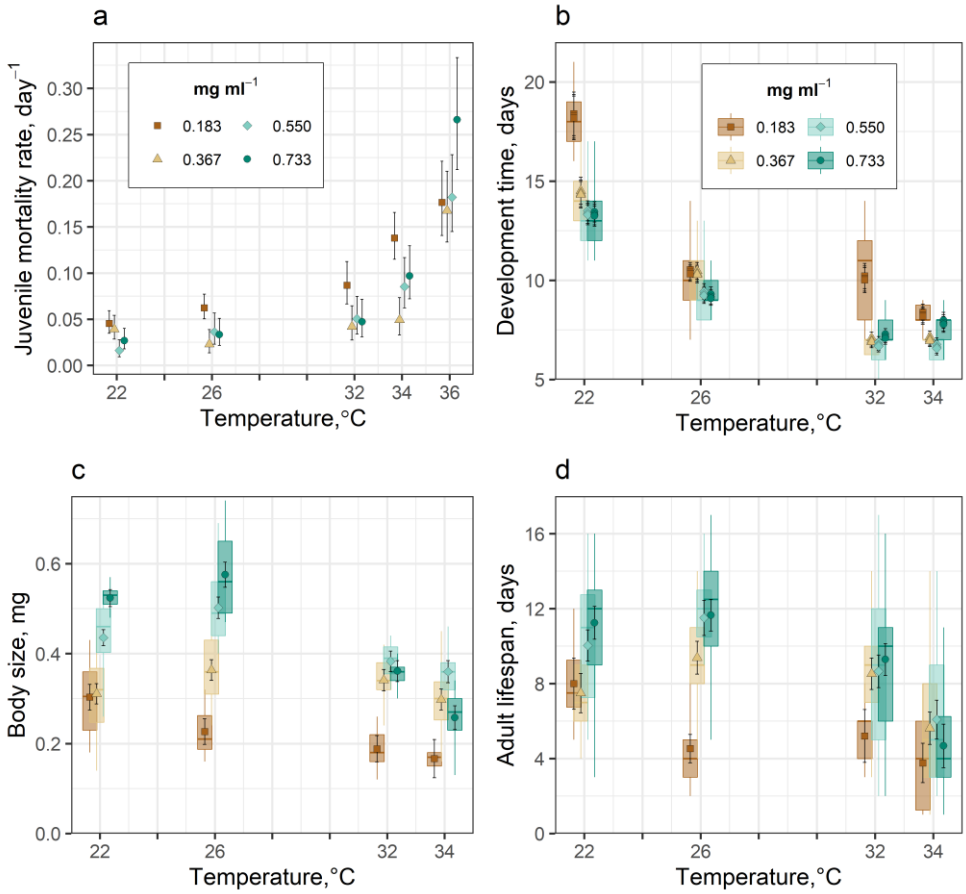

Fig. 1 | The effect of intraspecific larval competition on fitness traits in *Ae. aegypti* with 95% credible intervals (CIs). a, Intensified competition at low resource concentration (0.183 mg ml^{-1}) increased the negative effect of increased temperature on juvenile mortality. The CIs for 0.183 mg ml^{-1} and 0.367 mg ml^{-1} do not overlap, indicating a significant effect of competition on this trait's thermal response between these treatments, as temperatures increased from 22 to 34°C. **b**, Development time decreased with temperature at all resource levels, but, at most temperatures, it was significantly extended by intensified competition at low resource concentration. **c**, As temperatures increased from 22°C, intensified competition at 0.183 mg ml^{-1} significantly reduced size at emergence. **d**, As temperatures increased from 22 to 32°C, intensified competition at 0.183 mg ml^{-1} significantly reduced adult lifespan. Symbols denote the regression estimated means with 95% CIs calculated from the standard errors (Table S2) for the resource levels at each temperature. The resulting ANOVAs of the regressions for each trait are presented in Table S1. 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.

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Population fitness

At all resource levels, r_m responded unimodally to temperature. However, intensified competition at low resource concentration (0.183 mg ml^{-1}) significantly depressed r_m across the entire temperature range (Fig. 2a) and caused it to peak at a significantly lower temperature than at our intermediate resource concentration (0.367 mg ml^{-1}; Fig. 2b, Table 1). Intensified competition at low resource concentration also significantly narrowed the thermal niche width for r_m compared to when competition was relatively relaxed due to higher resource levels (Fig. 2a, Table 1).

At low resource concentration, r_m was negative until temperatures increased to 23.3°C (95% credible interval [CI]: 22.4–24.9°C, Fig. 2, Table 1). At this resource level, r_m reached a peak of 0.05 at its T_{opt} (26.6°C); it then declined to negative growth at 30.1°C ([CI]: 28.6–31.2°C). The breadth of r_m's thermal niche width at low resource concentration was 6.8°C ([CI]: 3.7–8.8°C).

In contrast, at the intermediate food level (0.367 mg ml^{-1}), r_m became positive as temperatures increased to 18.8°C ([CI]: 17.1–20.2°C), and it was maximal at 33.0°C (0.24, Fig. 2, Table 1). At 0.367 mg ml^{-1}, r_m declined to negative growth at 35.4°C ([CI]: 35.4–35.5°C). The thermal niche width for r_m at this resource level was 16.6°C ([CI]: 15.3–18.4°C). Overlapping CIs indicate that the predicted differences between the intermediate resource level and the higher resource levels (0.550 and 0.733 mg ml^{-1}) in r_m at T_{opt}, T_{opt}, and the thermal niche width were non-significant (Fig 2, Table 1).

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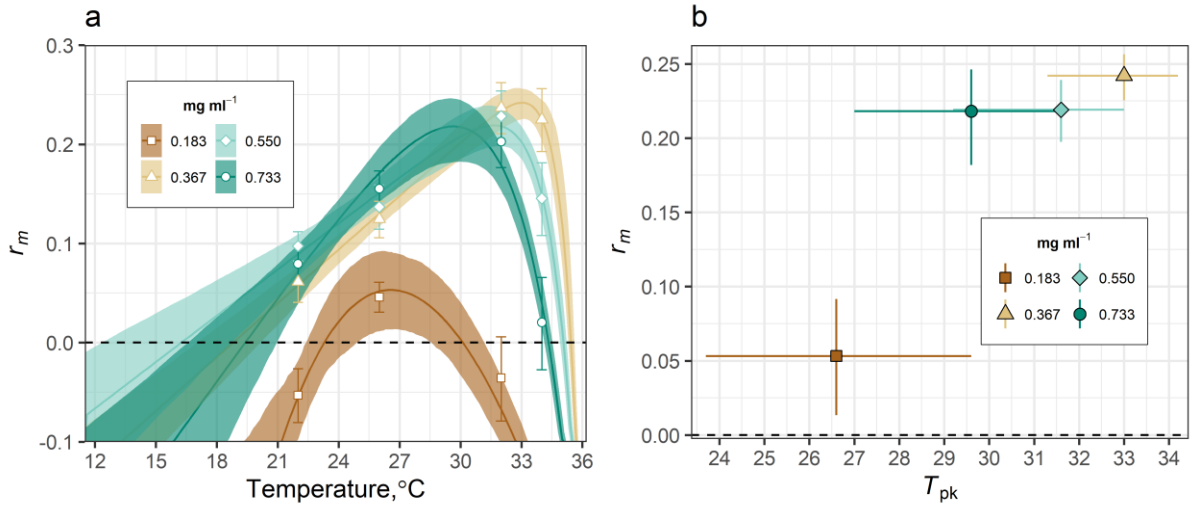

Fig 2 | The effect of larval competition on the thermal response of population-level *Ae. aegypti* fitness (r_m) with bootstrapped 95% prediction bounds. **a,** Intensified competition at low resource concentration (0.183 mg ml^{-1}) significantly depressed r_m across the entire temperature range and narrowed its thermal niche width compared to the higher resource levels (non-overlapping 95% prediction bounds, Table 1). Symbols denote matrix projection estimates with 95% confidence intervals. **b,** Competition at 0.183 mg ml^{-1} significantly (non-overlapping 95% confidence intervals) lowered maximal r_m and caused it to peak at a significantly lower temperature than at the intermediate resource level (0.367 mg ml^{-1}). Predicted r_m T_{opt} at 0.183 mg ml^{-1} indicates that competition could decrease r_m T_{opt} by 6.4°C, when compared to the intermediate resource level (0.367 mg ml^{-1}, Table 1).

Resource concentration (mg ml^{-1})	**r_m at T_{opt}** (± 95% CI)	**T_{opt} (°C)** (95% CI)	**T_{min} (°C)** (95% CI)	**T_{max} (°C)** (95% CI)	**Thermal niche width (°C)** (95% CI)
0.183	0.05 ± 0.04	26.6 (23.7 - 29.6)	23.3 (22.4 –24.9)	30.1 (28.6 – 31.2)	6.8 (3.7 – 8.8)
0.367	0.24 ± 0.02	33.0 (31.3 - 34.2)	18.8 (17.1 – 20.2)	35.4 (35.4 – 35.7)	16.6 (15.2 – 18.6)
0.550	0.22 ± 0.02	31.6 (29.2 - 33)	16.2 (12.4 – 18.6)	35.1 (35.0 – 35.3)	18.8 (16.4 – 22.9)
0.733	0.22 ± 0.03	29.6 (27.0 - 31.5)	19.4 (16.6 – 21.0)	34.3 (34.2 – 34.6)	14.9 (13.2 – 18)

Table 1 | Parameter estimates of the Thermal Performance Curves of r_m by resource concentration. Non-overlapping 95% Confidence Intervals (CIs) indicate that intensified competition at low resource concentration (0.183 mg ml^{-1}) significantly depressed maximal growth (r_m at T_{opt}) compared to the higher resource levels. Intensified competition at 0.183 mg ml^{-1} caused a significant decrease in r_m T_{opt} compared to r_m T_{opt} at 0.367 mg ml^{-1}. Competition at 0.183 mg ml^{-1} also caused a significantly narrower thermal niche width compared to the higher resource levels.

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Elasticity analysis

Juvenile survival was the most important contributor to r_m (Fig. S4). For example, at low resource concentration at 26°C, a 0.5 proportional increase in juvenile survival would increase rate of increase from 0.046 to 0.063 (Fig. S4d). In contrast, for the same treatment, a proportional increase of the same magnitude for adult survival would increase r_m from 0.046 to 0.050 (Fig. S4e), and fecundity would increase r_m from 0.046 to 0.048 (Fig. S4f). This underlines how the temperature-dependence of r_m derives mainly from how intensified competition at low resource concentration 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_m, which suggests that the carry over effect of reduced size at maturity on r_m is relatively weak.

DISCUSSION

Using a trait-based approach, laboratory experiments and mathematical modelling, we have shown that intraspecific larval competition in depleting resource environments can significantly change the shape of the r_m thermal performance curve. Differences between the thermal response of underlying r_m traits at low resource concentration versus the higher resource levels resulted in a marked divergence of the temperature-dependence of r_m between the four resource levels (Fig. 2).

Intensified competition at low resource concentration (0.183 mg ml^{-1}) significantly depressed r_m across the entire temperature range, caused a significant decrease in r_m T_{opt} compared to the intermediate food level (0.367 mg ml^{-1}), and significantly narrowed the thermal niche width compared to the higher resource levels (Fig. 2, Table 1). This indicates that population fitness becomes increasingly, and non-linearly constrained by larval competition as temperatures and resource depletion rates increase. This suggests that intraspecific competition is strongest at temperatures that are optimal for population growth.

The elasticity analysis shows that the primary mechanism underlying the divergent temperature-dependence of r_m across resource levels is decreased juvenile survival at low resource concentration (Fig. S2). This effect derived from how intensified larval competition

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at low resource concentration increased juvenile mortality rate and development time, which decreased population-level reproductive output and delayed the onset of reproduction.

Fecundity and adult lifespan had comparatively negligible effects on r_m, which suggests that the carry over effect of reduced size at maturity on r_m is relatively weak. For example, at low resource concentration, body size, adult lifespan and lifetime fecundity were greater at 22°C than at 26°C, yet fitness at 26°C was predicted to be over 200% higher (Figs. 1, S2a and b, S3a and b, Table S2). This is because the increase in temperature from 22 to 26°C decreased development time at 26°C (Fig. 1a, b). This increased juvenile survival at 26°C, leading to increased fitness as greater numbers of individuals could contribute to population growth through reproductive output. This is consistent with general studies of ectotherm fitness (Amarasekare and Coutinho 2013, Huey and Berrigan 2001), including mosquitoes (Huxley et al. 2020). This key finding implies that predictions about the effect of climatic warming on ectotherms, including disease vectors and transmission (which are generally from populations under high- or optima resource supply) likely underestimate the effect of temperature on development time and juvenile survival, and overestimate effects of temperature on lifespan and fecundity.

The trait-level responses of our higher resource concentration treatments correspond with studies that have synthesised laboratory-derived trait responses to temperature to estimate vector fitness and disease transmission. In these studies, the juvenile development rate of most mosquito vectors is expected to increase from ~0.07 day^{-1} at 22°C to ~0.14 day^{-1} at 32°C (Mordecai et al. 2019). In the present study, development rate (1/development time; Fig. 1b, Table S2) increased by a similar margin. For example, development rate at 0.550 mg ml^{-1} increased from 0.07 day^{-1} at 22°C to 0.15 day^{-1} at 32°C. In contrast, at low resource concentration, we found juvenile development rate increased from 0.05 day^{-1} at 22°C to 0.12 day^{-1} at 32°C (Fig. 1b, Table S2). Although these differences in juvenile development rate may appear small, we show that they can have dramatic effects on the temperature-dependency of r_m when combined with the negative impact of intensified competition on juvenile survival (Fig. 1a, Table S2).

Juvenile mortality rate increased significantly with temperature and it was consistently higher at low resource concentration (Fig. 1a) than at higher resource levels. This is probably because somatic maintenance costs increase with metabolic rate (Kooijman 2000), which

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cannot be met below a threshold resource supply level. Intensified competition at low resource concentration is likely to have prevented some individuals from meeting this increased energy demand, which explains why juvenile mortality rates were highest at 32 and 34°C at low-resource concentration (except at 36°C where no individuals survived at all) where the energy supply-demand deficit was expected to be the largest.

Because we show that the r_m TPC significantly changes shape in response to larval competition, r_m TPCs that are measured without competition effects (e.g. Deutsch et al. 2008, Vasseur et al. 2014) maybe less useful for predicting the consequences of future climatic warming on holometabolous insects than currently thought. More specifically, the profound effect of intensified larval competition at low resource concentration on the temperature-dependence of r_m is likely to substantially alter predictions about the temperature-dependence of vector-borne disease transmission. This underlines the importance of considering the effects of larval competition in depleting resource environments, in particular, when predicting the responses of ectothermic disease vectors to climatic warming.

In nature, populations likely experience intermittent resource depletion (Ostfeld and Keesing 2000, Wright 1983, Yee and Juliano 2012), but very few studies have examined how intraspecific competition in such environments can affect the r_m TPC. For example, in mosquitoes, field and laboratory studies have examined how resource availability and larval density interact to affect fitness (Gilpin and McClelland 1979, Gimnig et al. 2002, Heath et al. 2020, Walsh et al. 2013), while others have investigated the effect of resource availability and larval density separately (Romeo Aznar et al. 2018, Shapiro et al. 2016). However, none of these studies have considered environmental temperature. On the other hand, studies that have considered temperature have not considered resource depletion (Huxley et al. 2020), or how the effects of temperature and resource availability together affect fitness through traits (Couret et al. 2014, Padmanabha et al. 2012). As such, our study addresses an important gap by showing that the interactive effects of temperature and resource depletion should also be considered in studies of ectotherm population dynamics.

Since resource depletion can mediate the regulatory effects of larval competition on the temperature-dependence of r_m, it is also important to determine the temperature-dependence of resource availability itself (Huey and Kingsolver 2019). For example, recent studies show that mosquitoes can be reared exclusively on cultures of *Asaia* bacteria (Chouaia et al. 2012,

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Souza et al. 2019), that microbiota at mosquito breeding sites is spatially heterogenous (Hery et al. 2021), and that larval exposure to microbial variability can affect adult mosquito life history traits (Dickson et al. 2017). Microbial growth rates also increase with temperature to some optimum, so the concentration of food in the environment may also increase (Craine et al. 2010, Cross et al. 2015, Smith et al. 2019).

If resource availability increases with climatic warming, its regulatory effect on population growth could be relaxed through increased juvenile development and adult recruitment rates. Indeed, increased food availability with warming could contribute to the expansion of disease vectors and other invasive insect species into regions that were previously prohibitive by broadening r_m's thermal niche width (Amarasekare and Simon 2020). On the other hand, evidence from our high resource concentration treatments (e.g. a lower T_{opt} at 0.733 than at 0.367 mg ml^{-1}) may suggest that warming could have a negative impact on population growth by causing resources to be overabundant, which could lead to eutrophication and hypoxia in aquatic environments (Liikanen et al. 2002).

Alternatively, if climate change reduces the quantity of food available to ectotherms, their spatiotemporal ranges could contract (Huey and Kingsolver 2019, Lister and Garcia 2018). This is because, as we have shown here, intensified competition at low resource concentration prevents r_m from being positive at lower temperatures, decreases its optimal temperature, and forces it to become negative at lower temperatures. In this way, the effects of rising temperatures on insect populations could be especially pernicious, if food availability is simultaneously reduced (Huey and Kingsolver 2019).

We did not measure the effect of temperature and resource concentration on fecundity directly, but used the size-scaling of this trait to estimate this effect. This is because most of the effect of intensified larval competition at low resource concentration, is expected to affect adult mosquitoes indirectly by reducing size at emergence and lifespan (Briegel 1990, Steinwascher 1982). Despite these assumptions, we show that substantial under- or overestimation of fecundity by our size-scaling predictions and the use of starved adult lifespans, would not affect our main conclusions. This is because predicted fitness was relatively insensitive to these traits (Figs. S2, S3).

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Although the increased negative carry over effects of temperature and competition on adult traits may have had a relatively weak impact on fitness compared to juvenile traits, temperature × resource concentration interactions may have important effects on other components of vector-borne disease transmission (Parham et al. 2015). For example, smaller individuals may bite more frequently, which can increase transmission probability (Scott et al. 2000). Also, larval nutrition (Shapiro et al. 2016) and temperature (Shapiro et al. 2017) can independently influence within-vector parasite development, but future studies could consider how the combined effects of temperature and resource availability affect this, and other important transmission traits.

Studies on the effects of climatic change on resource availability have recently shown how warming could lead to the collapse of consumer populations due to increased phenological asynchrony with resource populations (Simmonds et al. 2020). However, while climatic warming is identified as the most important threat to insect populations (Halsch et al. 2021), very few field studies have considered how it may indirectly affect food availability. Therefore, our study underlines the importance developing accurate methods to measure how effective temperature-dependent fitness in the field is affected by the temperature-dependence of resource availability. Our study also underlines the importance of the effects of larval competition 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 how resource availability can mediate the effects of larval competition on the temperature-dependence of population fitness, and therefore ultimately, the effects of climatic variation on abundance dynamics in the field.

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