Sex differential effects of developmental heat stress on life-history and reproductive traits

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Abstract

Global warming has led to increased mean global temperatures with projections suggesting continued warming throughout this century, posing an escalating threat to biological systems worldwide. Ectotherms are most vulnerable to this change as heat stress conditions can have severe implications on their development, mating interactions, and fitness. However, the sex-specific effects of developmental temperature on these factors remain poorly understood. Here, we conducted an experiment using the decorated cricket, *Gryllodes sigillatus,* to disentangle sex-specific effects of developmental temperature on life-history, pre- and post-copulatory and fitness-related traits. Crickets were reared at two temperatures: a control temperature (27 °C) and a heat-stress temperature (36 °C) and their development was monitored. Post sexual maturation, mating assays were conducted in a full-factorial mating design, and after successful fertilization, reproductive output was quantified. We found that heat stress accelerated development to adulthood differentially in both sexes. Furthermore, we found that female developmental temperature affected mating latency, with heat-stressed females exhibiting longer latencies, suggesting that females exert control over this trait. Conversely, male developmental temperature affected courtship and copulation success. Heat-stressed males were less willing to initiate courtship and largely unsuccessful at transferring the spermatophore during mating. Post-copulation, heat stressed females took longer to feed on the nuptial gift. Moreover, the feeding time was also significantly predicted by the wet mass of both males and females, suggesting that gift consumption is driven by a combination of male-provided quality and the female's own energetic requirements. Lastly, we found that heat-stressed females exhibited significantly reduced fecundity and fertility, highlighting downstream reproductive costs of developmental thermal stress. Thus, our study highlights how developmental temperature alters life history, fertility, and can have sex-specific impact on shared mating traits.

Keywords: developmental thermal stress, mating behaviour, thermal plasticity, sex-specific effects, climate change

1. Introduction

Global warming has been leading to greater temperature variation and prolonged heatwaves. Ectotherms depend on the environmental temperature to regulate their body temperatures and are thus sensitive to external thermal changes. External thermal conditions influence various traits in ectotherms, like morphology, life history, behaviour, and physiology (Angilletta et al., 2003; Audzijonyte et al., 2016; Abram et al., 2017; Schulte et al., 2015). Ectotherms function within a permissive temperature range, where physiological and behavioural processes maintain homeostasis efficiently, and once a specific critical temperature is exceeded, they enter a stressful temperature range in which disruptive processes (such as cellular damage and metabolic imbalances) overtake the physiological processes that maintain homeostasis (Ørsted et al., 2022). Changes in ectotherm physiology due to environmental temperature ultimately affect life-history, morphological, behavioural, and reproductive traits (Kim et al., 2017; Ohlberger, 2017; Michelangeli et al., 2018; Porcelli et al., 2017). All of these together contribute to an individual's fitness and capacity to survive in variable environments. As heat stress has cumulative effects with exposure time within the stressful temperature range (Ørsted et al., 2022), it is important to understand how long-term heat stress impacts these traits.

Thermal stress during development can lead to lifelong alterations in insect morphology, metabolism and resource allocation (Leith et al. 2021; Neven, 2000). Changes in resource allocation, along with metabolic changes, may alter the rate at which insects develop into adults. Previous studies with different insects have shown that development rate is affected by changes in temperature (Garrad et al., 2015; Kong et al., 2024). Faster development may lead to a shift in energy investment, with a focus on maturing faster at the expense of adult nutrient reserve accumulation. According to Atkinson (1994), the temperature-size rule states that, for most ectotherms, an increase in temperature during development results in a reduction in body size, while a decline in temperature leads to an increase in adult body size. The relationship between the temperature at which organisms develop and their size is most thoroughly understood in arthropods (Hirst et al., 2015, Horne et al., 2015), especially in insects of the order Diptera (French et al., 1998). However, in some insect species, including the cricket *Acanthogryllus asiaticus* and the Asian lady beetle *Harmonia axyridis*, individuals reared at high temperatures have been found to be heavier than those reared at low temperatures (Singh et al., 2020; Knapp & Nedvěd, 2013). Thus, the extent to which the temperature-size rule applies across other insect orders remains understudied.

The ability to reproduce may be hindered by poor-quality gametes resulting from heat stress (Porcelli et al., 2017; Gruntenko et al., 2003), with thermal effects on fertility manifesting well before survival is compromised. Research has shown that the thermal fertility limit is reached long before the lethal thermal limit, underscoring that reproductive failure is among the earliest and most ecologically consequential costs of heat stress (Parratt et al., 2021; van Heerwaarden and Sgrò, 2021). Heat stress significantly impairs male fertility through reduced sperm production, decreased sperm motility, morphological sperm abnormalities, and reduced sperm density (Hansen, 2009; Nguyen et al., 2013; Hurley et al., 2018; Sales et al., 2018; Domenech and Fricke, 2023), and once a critical temperature threshold is crossed, males may become entirely infertile (Araripe et al., 2004; Sales et al., 2021). Female reproductive efficiency can be equally vulnerable. Heat stress is known to cause oocyte degeneration, defective vitellogenesis, and reduced ovary size which can collectively result in decreased fecundity (Krebs and Loeschke, 1994; Gandara and Barbosa, 2022; Kirk Green et al., 2019). Since female fecundity and fertility represents the primary bottleneck through which thermal stress can translate into reduced population reproductive output, understanding how developmental temperature specifically shapes female reproduction is essential for assessing the full reproductive cost of climate warming in ectotherms.

Reproductive success under heat stress may, in addition, be influenced by mating interactions. Mating interactions include mate attraction, courtship display, copulation, and post-mating behaviours (Ombuya et al., 2025). These mating interactions can be strongly influenced by both developmental temperature and environmental conditions (Leith et al., 2021; Macchiano et al., 2023). Several studies have demonstrated how temperature influences various aspects of mating interactions in several species (Patton and Krebs, 2001; Augustin et al., 2022; Katsuki and Miyatake, 2009; Bhaisare and Chaudhary, 2023; Smith et al., 2025). The role of these behaviours is highly significant when determining the reproductive outcome, which directly influences reproductive fitness. Although many researchers have studied the effects of temperature on reproductive traits, sex-specific consequences of thermal stress on mating behaviour remain comparatively understudied, with males and females rarely examined independently within the same experimental framework (Dougherty et al., 2023; Reinhold and Rizvi, 2026). Since mating interactions are shaped by contributions from both sexes, explicitly disentangling the effects of temperature on each partner's behavioural contribution is essential for understanding how heat stress impacts matings to ultimately shape reproductive fitness.

The decorated cricket, *Gryllodes sigillatus*, is a cosmopolitan species that serves as a model organism for studying thermal effects due to its tropical and subtropical distribution and the ease with which mating behaviours can be observed. The species is typically found in the temperature range of 20 °C to 30 °C (Smith and Thomas, 1988). During their development, these crickets pass through seven nymphal instar stages, after which they undergo the final moult and become adults (Kong et al., 2025). In *Gryllodes sigillatus*, mating behaviour starts with the male producing a distant calling song to attract the female. As the female gets closer, this calling song changes into a softer courtship song. If interested, the female mounts the male, and the male then initiates copulation (Figure 1). While copulating, the male transfers a spermatophore, which is composed of two parts: a gelatinous spermatophylax and a sperm containing ampulla. The female removes the spermatophylax and starts feeding on it immediately after mating, while sperm transfer occurs via the ampulla (Sakaluk, 1984). At this post-copulatory stage, the male guards the female (Figure 1). When the female finishes consuming the gift, she then bends to retrieve the ampulla left behind in the genital papilla and feeds on it. We selected *Gryllodes sigillatus* as an appropriate model species for investigating the influence of temperature on several attributes for both sexes, as earlier studies have demonstrated that developmental temperature can influence life-history traits and reproductive performance (Kong et al., 2024).

In this study, we investigate the sex-specific effects of developmental heat stress on life-history, morphology, mating traits and fertility in *Gryllodes sigilattus*. We reared crickets at two temperatures: a heat-stress treatment (36 °C; Kong et al., 2024) and a control treatment (27 °C; Rizvi et al., 2025) throughout development. We recorded the time to adulthood and the body mass of adults. Following sexual maturation, we conducted no-choice mating trials to disentangle sex-specific developmental temperature effects on pre- and post-copulatory mating interactions. To test the effect of developmental temperature on reproductive output, female fecundity and hatching success was assessed after copulation. We expected the development to be faster and body mass to increase under the heat-stress treatment, as observed in previous studies (Kong et al., 2024). We also hypothesized that the temperature treatment for the males would affect the courtship behaviour and copulation time, while the female temperature treatment would affect traits such as mating latency, mating success, nuptial gift feeding time, and fecundity. Furthermore, we hypothesized that male and female temperature treatments might interact in order to influence some shared mating traits (such as mating latency and mating success) and the reproductive output. Our study provides evidence on sex-specific developmental responses to thermal stress, offering critical insights into how organisms navigate the reproductive challenges imposed by rapid climate change.

2. Methods

2.1. Animal Rearing

To disentangle the effects of developmental temperature on mating behaviour and fertility, two experimental treatments, one of high-temperature (36 °C) individuals and another of control-temperature (27 °C) individuals, were developed. Laboratory population of *Gryllodes sigillatus* originated from a stock of approximately 200 individuals (adults and subadults) sourced from an insect breeder firm in April 2022 (ReptilienKosmos, Germany). Crickets were maintained in a laboratory room at 27 ± 1 °C on a 12:12 light: dark cycle. They were provided with ad libitum food (Nekton cricket breeding concentrate), water in a glass vial (22 ml) plugged with cotton wool, and egg cartons for shelter. Individuals for the experiment were sourced from the 12th generation of the lab population. Plastic cups filled with moist cotton wool were placed inside the population boxes to collect eggs for 1 week. Eggs were then counted and placed in separate incubators: one at 27 °C with a 12L:12D photoperiod and the other at 36 °C with a 12L:12D photoperiod to develop the treatments.

Once eggs started hatching, the number of hatchlings was counted. The hatchlings were placed into separate boxes (16.9 cm × 10.5 cm × 7.4 cm) with egg carton pieces, a vial of water (13mL) with cotton plug, and some food (Nekton cricket breeding concentrate). The hatchlings were then placed under the same environmental conditions in which they had hatched to complete further development. In order to maintain virgin populations, male and female nymphs were segregated as the ovipositor started to become visible in the females. Separation was conducted by administering a 1-minute carbon dioxide (CO2) shock to knock out the crickets, then transferring them to segregated boxes (16.9 cm × 10.5 cm × 7.4 cm).

Each box contained between 3 to 6 individuals at a time. Development of a total of 300 individuals (27°C males: 90, 27°C females: 81, 36°C males: 61, 36°C females: 61) was monitored. Once the males had moulted into adults, they were marked individually by placing a small dot of paint marker on their abdomen to identify them during mating trials. Post marking, the males were placed in a measuring cup, and their weights were measured using an electronic balance (Kern 770). Females were not marked, but were measured just before the mating trials and then placed directly into the mating arena.

2.2. Mating Trials

Mating trials were conducted in a full factorial design (Figure 2) and at a constant environmental temperature of 27 °C. Individuals reared at 36 °C were given up to 1 hour to acclimatize to the ambient temperature of 27 °C before the mating trials began. Additionally, a subset of heat stressed males and females (reared at 36 °C) were mated at an ambient temperature of 36 °C to tease apart the effects of developmental temperature and environmental temperature during mating. This allowed us to assess whether behavioural responses observed in heat-stressed individuals reflected lasting developmental effects or were instead modulated by the ambient thermal conditions experienced during the trial itself. The females from the treatment boxes were knocked down using carbon dioxide, weighed, and then placed individually in mating arenas (16.9 cm x 10.5 cm x 7.4 cm) with an egg carton piece. The marked males were individually placed in different cups after knocking them down with carbon dioxide. All individuals were then transferred to a dark room with red light, as crickets are insensitive to red light. A marked male was randomly selected and introduced into the mating arena. Once the male started singing, the stopwatch (ATP digital stopwatch TIM1166) was started, and the time taken for the female to mount the male after the first singing was recorded as a measure of mating latency. Immediately after the first mounting, the stopwatch was resumed to measure mating duration (the time the female remained mounted on the male until the transfer of the spermatophore). The stopwatch was paused whenever the female dismounted and resumed when she mounted again; these timestamps were recorded. Once sperm transfer was complete, the stopwatch was resumed when the female began feeding on the nuptial gift and stopped once she finished.

Each pair was given a maximum of 15 minutes to initiate mating, after which the partners were changed. Partners were changed by replacing the focal male with a different-marked male in the mating arena with the female. If an individual was unable to mate successfully despite trying with five different partners, they were not used for any further trials. All mating trials were conducted at least 1 week after the final moulting, to ensure the individuals were sexually receptive.

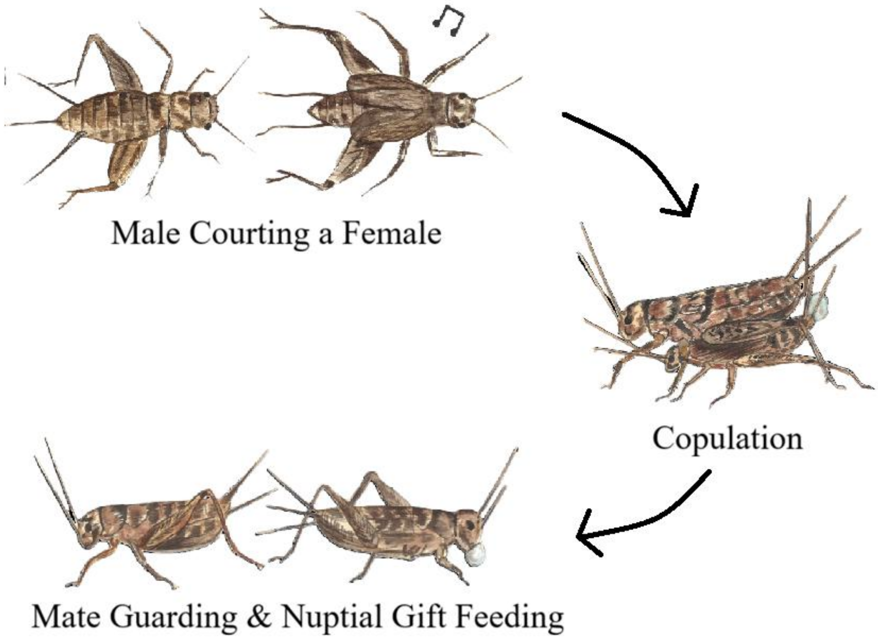


Figure 1: *Simplified illustration of mating system of Gryllodes sigillatus*

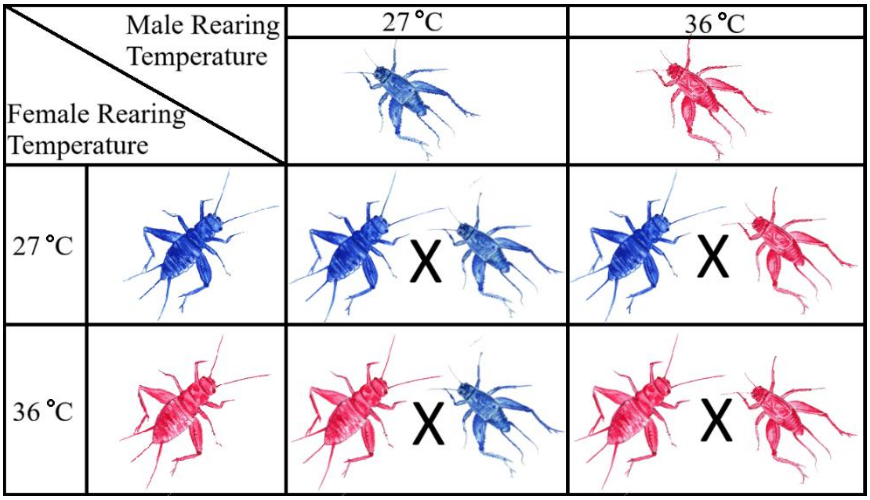


Figure 2: *Full-factorial mating crosses conducted at an ambient temperature of 27 °C*

2.3. Female Fecundity and Fertility Measurements

After a mating trial was successfully completed, the male was removed from the arena to prevent further matings. The females were given a piece of egg carton, food (Nekton cricket breeding concentrate), a water vial (13mL) with a cotton plug, and an egg pad (a cup containing damp cotton wool) to serve as an oviposition substrate. All the females were placed in incubators at 27 °C with a 12L:12D photoperiod for egg laying. Each female was kept in the incubator for 3 weeks during egg-laying. The eggs were collected from the pads weekly and counted under a stereo microscope (Leica MS5, 1.6x magnification), and the pads were then replaced with fresh ones. The collected eggs were counted, covered with wet cotton, and placed in separately labelled boxes (16.9 cm × 10.5 cm × 7.4 cm). They were then kept in the incubator for hatching at an ambient temperature of 27 °C and a photoperiod of 12L:12D. Only the eggs laid by the females during the first two weeks were incubated. Eggs laid in the third week were counted, then frozen overnight and discarded. Once hatchlings emerged, they were counted, frozen, and discarded. Each box containing eggs was kept for up to 3 weeks to detect any signs of hatching. If no hatchlings were obtained within 3 weeks, they were discarded. In boxes from which hatchlings were obtained, the boxes were kept in the incubator for a period of 1 week post the final hatching, after which the remaining eggs were discarded.

2.4. Statistical Analyses

2.4.1. Development Time and Wet Mass

Statistical analysis was performed in R version 4.5.2 (R Core Team 2025). Data processing and the conversion of group-level observations to individual-level records were conducted using *tidyverse* (Wickham et al., 2019), with duration calculated via *lubridate* (Grolemund and Wickham, 2011). To analyze development speed, we conducted survival analysis using *survival* (Therneau 2026) and *survminer* (Kassambara et al., 2025). Specifically, to resolve issues of monotone likelihood and provide stable estimates for temperature effects, we used Firth's Penalized Likelihood Cox Regression via the *coxphf* package (Heinze et al., 2023). This allowed for the calculation of Hazard Ratios (HR) to compare the relative rate of adult emergence between rearing temperatures and sexes. For adult wet mass, a linear model was used to check for the effects of temperature, sex, and their interaction. The model was tested using the *DHARMa* (Hartig, 2024) package to simulate residual diagnostics to assess normality, homoscedasticity, and the presence of outliers. Post-hoc pairwise comparison for both development time and wet mass was conducted using the *emmeans* package (Lenth and Piaskowski, 2025). Data visualization was conducted using *ggplot2* (Wickham 2016), *patchwork* (Pederson, 2025), *ggsignif* (Eltze et al., 2021), and *ggpubr* (Kassambara 2025).

2.4.2. Mating Trials and Reproductive Output

All statistical analyses were performed in R version 4.5.2 (R Core Team 2025), with packages loaded via *pacman* (Rinker and Kurkiewicz, 2017) to ensure a streamlined workflow. The analyses were based on 462 mating trials conducted across all experimental treatments. We fit generalized linear mixed-effects models, linear mixed models using *lme4* (Bates et al., 2015) or *glmmTMB* (Brooks et al., 2017), or Bayesian models using *brms* (Bürkner, 2017), depending on the data and error structure. For all models (unless stated otherwise), male developmental temperature, female developmental temperature, and their two-way interaction were included as fixed effects, while individual ID was included as a random effect. Male and female wet mass were included as covariates in all relevant analyses. All models were tested using the *DHARMa* (Hartig, 2024) package to simulate residual diagnostics to assess normality, homoscedasticity, and the presence of outliers. The effect of thermal stress on the probability of male courtship was analysed using a Bayesian model with a Bernoulli distribution. Since mating latency data (in seconds) were right-skewed, we applied a log transformation to improve the normality of the residuals and stabilize the variances. For mating duration data (in seconds), the data were rank-transformed prior to analysis to accommodate non-normality and outliers. To test for correlation among some factors in each pair, a Pearson correlation test was used.

For post-copulatory traits like nuptial gift feeding duration, female fecundity and fertility, due to insufficient data from the other two crosses as a result of high mating failure, only the 27 °C males x 36 °C females and 27 °C males x 27 °C females crosses were considered. Feeding duration was analysed using female developmental temperature as a predictor, with female and male wet mass as covariates. As the individuals were not repeated, random effects were not included in the model. Furthermore, using the *car* (Fox and Weisberg, 2019) package, Levene's Test was conducted to assess homogeneity of variance across the two female treatments. We fitted a negative binomial generalized linear model to analyse the number of eggs laid (in two weeks), with female developmental temperature as the main predictor and scaled female wet mass as covariate. We modelled egg hatching success for week 1, week 2, and the total of both using beta-binomial generalized linear models fitted with *glmmTMB*. To test the effects of environmental temperature during mating, we used data from the 36 °C male x 36°C female crosses conducted at an ambient temperature of 36 °C and 27 °C. Data visualization was performed using *ggplot2* (Wickham 2016), *ggsignif* (Eltze et al., 2021), *ggpattern* (FC and Davis, 2026), *patchwork* (Pederson, 2025), and *ggpubr* (Kassambara 2025). Post hoc comparisons of main level effects and interactions were performed using the function emmeans in the ‘*emmeans*’ package (Lenth and Piaskowski, 2025).

3. Results

3.1. Effect of Rearing Temperature on Development Time and Wet Mass

Temperature significantly affected the time required for hatchlings to mature into adults. Crickets reared at 36 °C developed nearly twice as fast as those at 27°C (Firth’s Cox PH: HR = 1911.69, p < 0.001, Figure 3a, ST 1). The median development time was 39 days (95% CI: 38–40) at 36°C compared to 76 days (95% CI: 74–77) at 27°C. Sex also played a significant role in developmental rate (HR = 0.72, p < 0.01, ST 1); males exhibited a slower developmental pace than females at both temperature treatments. At 27°C, males reached adulthood at a median of 76 days (95% CI: 74–80) compared to 75 days for females (95% CI: 72–77). At 36°C, this gap widened, with males requiring a median of 41 days (95% CI: 39–42) versus 38 days for females (95% CI: 36–40). Developmental temperature had a significant effect on female wet mass (β = 0.077, SE = 0.009, t = 7.82, p < 0.001, Figure 3b, ST 2), with females reared at 36°C being significantly heavier than those reared at 27°C. In contrast, developmental temperature had no significant effect on male wet mass (t = 0.372, p = 0.710, Figure 3b, ST 2).

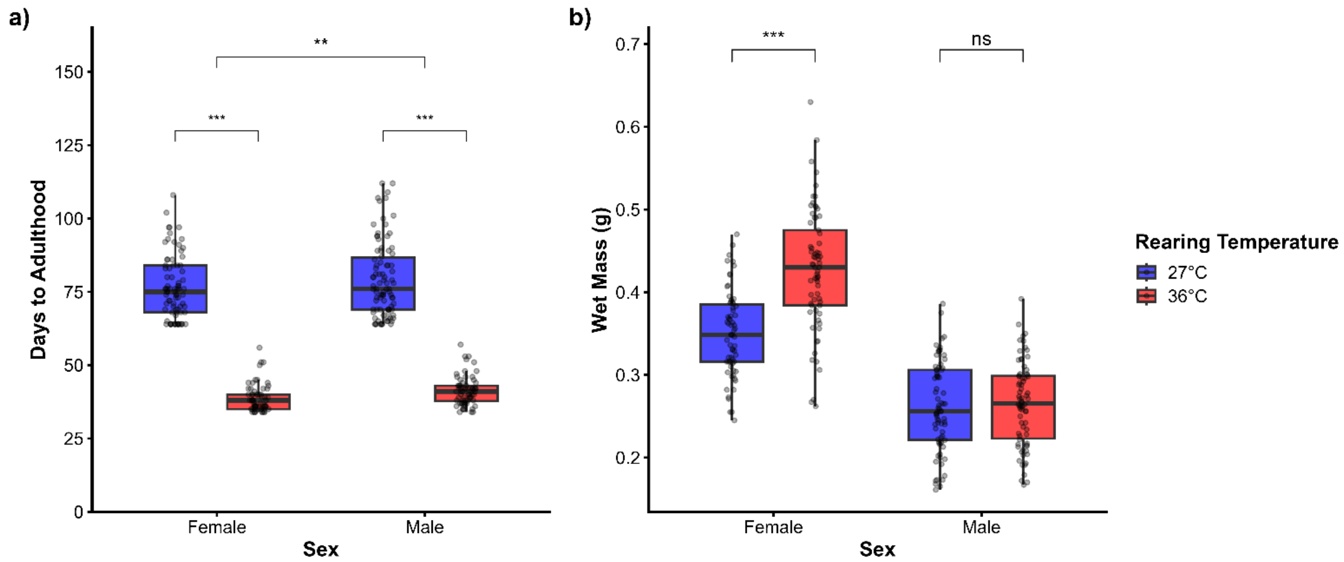


Figure 1: *Effect of rearing temperature on (a) time taken to reach adulthood and (b) wet mass. Females showed a significant increase in wet mass with higher developmental temperature. Horizontal bars indicate the median.*

3.2. Effect of Developmental Temperature on Courtship

Male developmental temperature had a strong negative effect on the probability of courting (β = 0.45, 95% credible interval [CI] = [-7.06, -2.99], Figure 4a), with males reared at 36 °C being less likely to court females than those reared at 27 °C. On the other hand, female wet mass had a positive effect on the probability of being courted (β = 0.45, 95% credible interval [CI] = [0.04, 0.87], Figure 4b), with females having higher wet mass being more likely to be courted by males. There was no significant effect of male wet mass, female developmental temperature, or the interaction between the two temperature treatments on courtship probability (ST 3). Additionally, male courtship initiation led to female mounting in 95.7% of cases across all treatment groups ($p < 0.001$). Fisher's exact test confirmed that the high probability of an attempt following courtship did not differ significantly across the four temperature treatments ($p = 0.14$, Figure 4c)

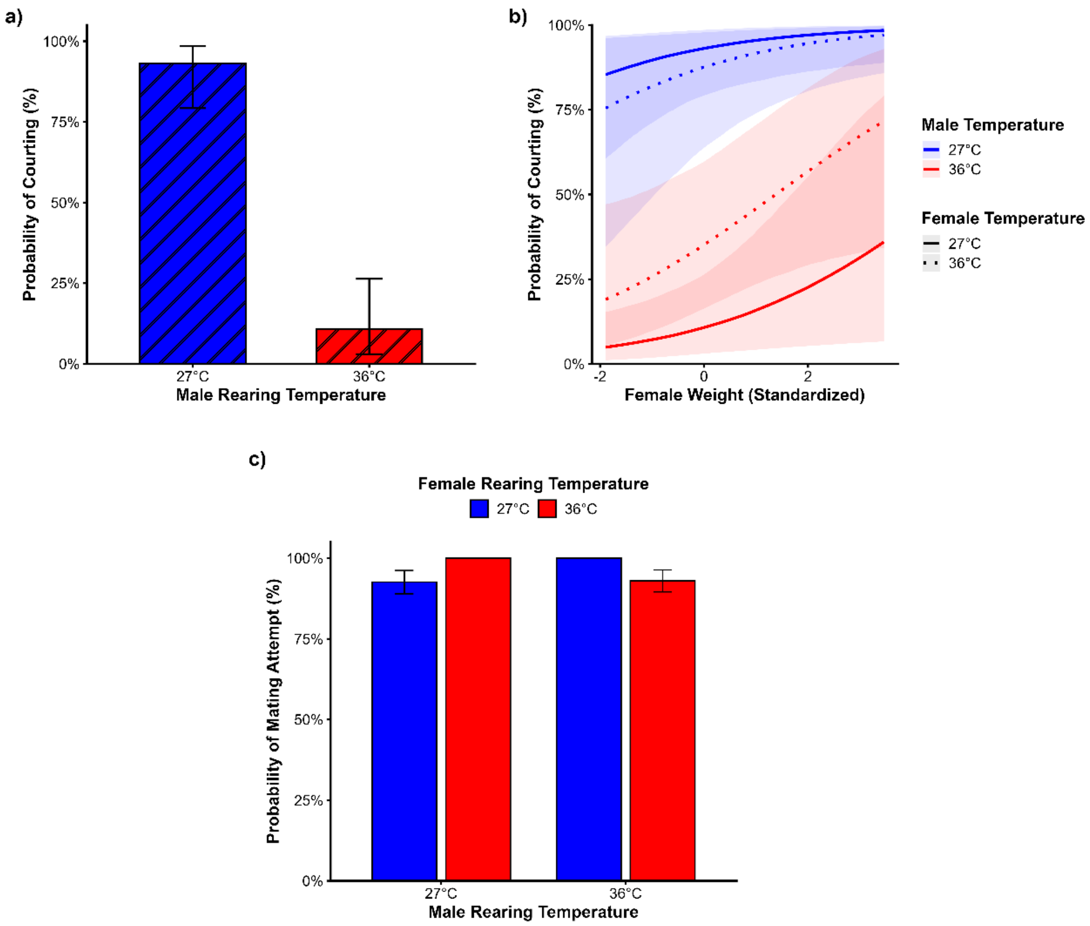
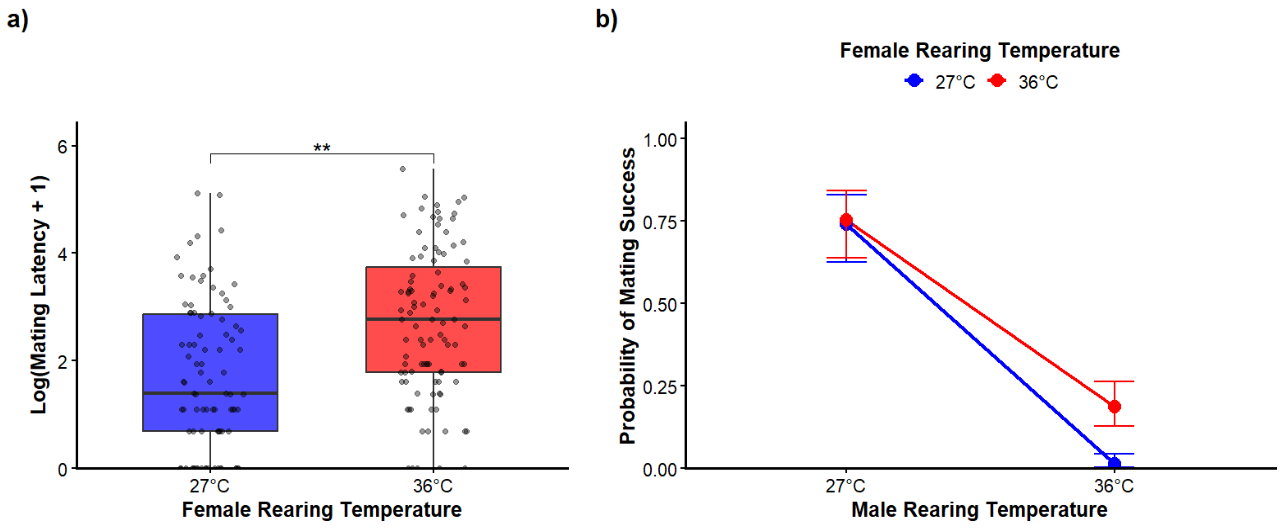


Figure 2: *Effect of developmental temperature on courtship behaviour and mating attempt. (a) Males developed at 36 °C show a decreased probability of courting females as compared to those developed at 27 °C. Solid bars represent the posterior mean probability calculated by the Bayesian model. Vertical error bars represent the 95% Credible Intervals (CI), indicating the range with 95% probability in which the true population means reside. (b) Heavier females experience a higher probability of being courted by males than lighter females within the 15-minutes observation period. (c) Probability of a female mounting a male across all temperature treatments post-male courtship initiation. Vertical error bars indicate ± 1 SE.*

3.4. Effect of Developmental Temperature on Mating Latency and Mating Success

Mating latency was significantly affected by female temperature treatment ($\beta = 0.99$, SE = 0.36, $p < 0.01$, Figure 5a), with females reared at 36 °C exhibiting longer mating latencies compared to those reared at 27 °C. Male and female wet mass, male developmental temperature, and the interaction between the male and female treatments had no significant effect on the mating latency (ST 4). Mating success was significantly influenced by male developmental temperature (β = - 5.26, SE = 1.36, p < 0.001, Figure 5b), with males reared at 27 °C being much more successful in transferring a spermatophore to the female than those reared at 36 °C. Although as a main effect female developmental temperature did not have a significant effect on mating success (p = 0.92), a significant interaction was observed between the male and female temperature treatments (β = 2.66, SE = 1.32, p = 0.04, Figure 5b), with males reared at 36 °C being more successful in transferring spermatophore to females reared at 36 °C, than with females reared at 27 °C. Male and female weights did not significantly affect mating success (ST 5). There were also no detectable effects of any predictors on mating duration.



Note: Vertical bars in (b) represent ±1 SE (retransformed from logit scale)

Figure 3: *Effect of developmental temperature on mating latency and mating success. (a) Females reared at 36 °C exhibit longer mating latencies than those reared at 27 °C. Horizontal bars represent the median log-transformed mating latency. (b) Males developed at 36°C were more successful in mating with females developed at 36°C than those developed at 27°C. Overall, males developed at 36°C were less successful in sperm transfer than those developed at 27°C. Asymmetry between the lines represents an interaction effect.*

3.5. Effect of Female Developmental Temperature on Nuptial Gift Feeding Duration

Female developmental temperature significantly influenced feeding duration, with females reared at 36°C taking longer to feed on the nuptial gift than those reared at 27°C (β = 1004.90, SE = 404.10, t = 2.49, p = 0.016, Figure 6). Furthermore, feeding duration was significantly affected by both female and male mass. Female wet mass was a significant negative predictor (β = -6.47, SE = 2.60, t = -2.49, p = 0.016, S1), whereas male wet mass was a significant positive predictor (β = 7.91, SE = 2.91, t = 2.71, p = 0.009, S1). A post-hoc Levene's test indicated that the variance in feeding behaviour was also significantly affected by temperature ($F_{1,53}$ = 7.88, p < 0.01) as females raised at 36 °C showed greater variance in their feeding duration than those raised at 27 °C.

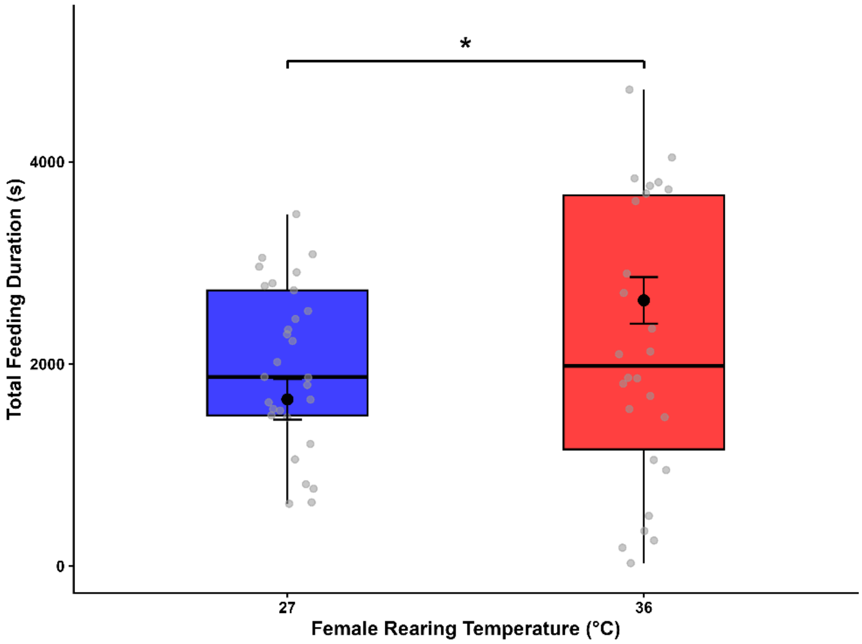


Figure 6: *Total nuptial-gift feeding duration between female developmental temperature treatments (n=55). Plot shows that heat stressed females took longer to feed than control ones. Boxplots show the interquartile range and median, grey points represent raw data and black points with error bars indicate model adjusted means with 95% CI.*

3.6. Effect of Female Developmental Temperature on Fecundity and Fertility

Developmental temperature significantly affected female fecundity, with females reared at 36°C laying fewer eggs than control females reared at 27°C (β = -0.46, z = -2.71, p = 0.006, Figure 7a). Female wet mass was also a significant positive predictor of fecundity (β = 3.46, z

= 3.21, p = 0.001, Figure 7a), indicating that heavier females produced more eggs. Female developmental temperature also had a significant effect on fertility (β = -1.23, SE = 0.32, p < 0.001, Figure 7b, ST 6), with females reared at 27 °C having greater fertility than those reared at 36 °C. Additionally, eggs laid in the first and second week post-mating by females reared at 27 °C had a higher success of hatching (Week 1: β = -1.05, SE = 0.41, p < 0.01, S2, ST 6; Week 2: β = -1.32, SE = 0.42, p < 0.01, S2, ST 6) compared to eggs laid by females reared at 36 °C.

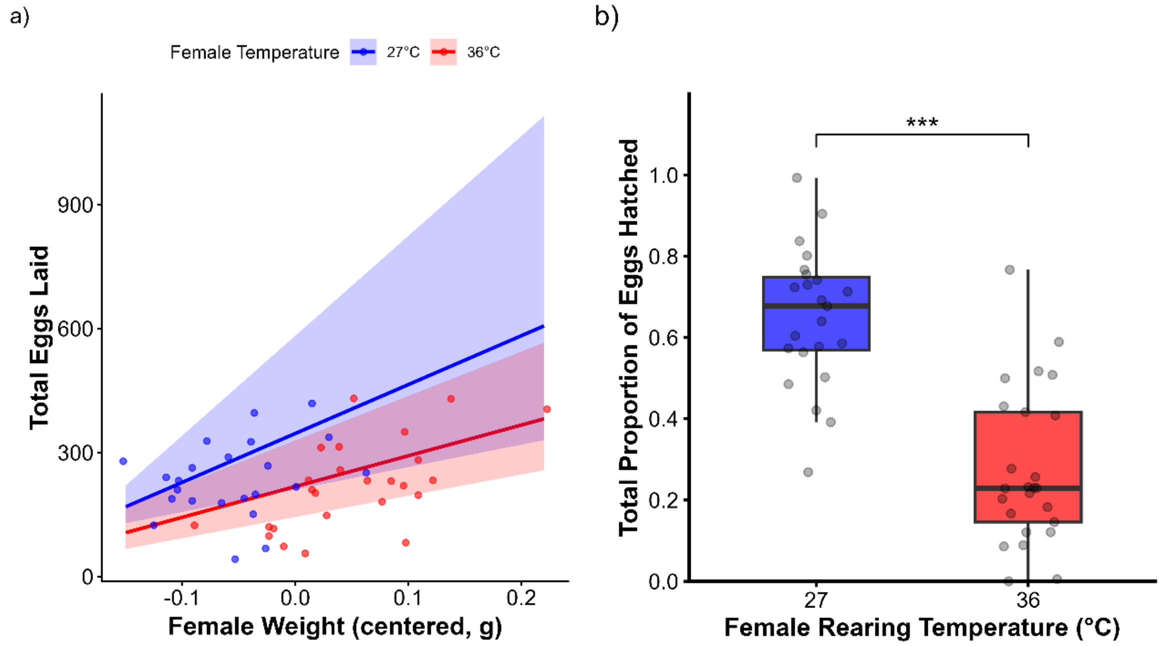


Figure 7: *Effect of developmental temperature on female reproductive output (n=49). a) Plot indicates a significant negative effect of female rearing temperature on fecundity, independent of the observed variation in female body weight. The regression lines and shaded 95% confidence intervals are derived from a negative binomial generalized linear model, showing predicted egg counts as a function of female body weight b) Females reared at 27 °C have greater fertility than those reared at 36 °C when successfully mated with control males. Horizontal bars indicate the median proportion of eggs hatched, and boxes indicate the interquartile range.*

3.7. Effect of Environmental Temperature on Mating Behaviour

Mating trial temperature had no detectable effects on probability of male courtship, mating latency, probability of mating attempt, mating duration and copulation success in heat stressed individuals (reared at 36 °C). The only two traits where we detected a significant effect of trial temperature were number of mating attempts and nuptial gift feeding duration. There was an increased mating attempt frequency at 36°C compared to 27°C ($z = 2.56$, $p = 0.01$, S3). Neither male nor female wet mass significantly influenced the number of mating attempts (ST 7). Females mated at 36 °C had shorter feeding duration than those mated at 27 °C ($t_{15.2} = -2.43$, $p = 0.03$, S4). Additionally, male wet mass positively affected feeding duration ($\beta = 536.39$, $p = 0.03$, S5), while female weight had no detectable effect (ST 8).

4. Discussion

In this study, we investigated the sex-specific effects of developmental temperature on life-history traits, morphological traits, mating behaviour, and reproductive output by conducting fully factorial, no-choice mating trials. We found that both male and female developmental temperatures affected development rate and mating behaviours differentially. Our results also show that developmental temperature affected wet mass and reproductive output of females. Lastly, we could tease apart the effects of developmental and environmental temperature on mating behaviour in heat stressed crickets, showing that environmental temperature can also alter certain mating behaviours.

4.1. Effect of Developmental Temperature on Life History and Adult Morphology

Developmental temperature strongly influenced life-history and body mass trajectories in *Gryllodes sigillatus*. The crickets developed faster when reared at 36 °C than at 27 °C, a common pattern among many ectothermic organisms (Lee et al., 2013; Ruthsatz et al., 2018; Ciordia et al., 1963; Lazo and Pita, 2012; Paul, 1998; Kong et al., 2024). Additionally, across both temperature treatments, females developed faster than males. This pattern aligns with broader evidence for sex-specific developmental scaling in insects, where females prioritize faster maturation to enhance reproductive opportunity (Degen et al., 2015). Thermal performance curves (TPCs) show how rates of biological processes increase exponentially with temperature up to a critical thermal optimum, beyond which performance rapidly declines, highlighting how an ectotherm's body temperature affects its performance and fitness (Sinclair et al., 2016). The accelerated development at 36 °C captures the ascending phase of the curve, and as Kong et al. (2024) showed, beyond 36 °C, the development of *G. sigillatus* becomes impaired; it is likely that 36 °C represents the critical thermal optimum for these crickets.

The temperature-size rule states that ectotherms developing under higher temperatures are relatively smaller due to a disproportionate effect of temperature on the growth and development rates (Atkinson, 1994). However, our results show an exception to this rule, female *G. sigillatus* were larger when reared at 36°C compared to 27°C. While large body size generally correlates with increased fitness in ectotherms (Kingsolver and Huey, 2008), this result suggests selection for size may intensify under thermal stress, a pattern previously noted in other orthopterans (Walters and Hassall, 2006). Our finding of increased female mass at 36°C partially aligns with Kong et al. (2024), however, we found no significant treatment effect on male mass. This discrepancy likely stems from differences in measurement timing; we measured mass within two weeks of adult eclosion, whereas Kong et al. (2024) averaged measurements over four weeks. Given that insect body mass is dynamic and known to fluctuate post-eclosion (Sturm, 2024), the lack of a significant difference in males may reflect different rates of mass loss between treatments early in adulthood. Ultimately, the sex-specific response in body mass suggests divergent selection pressures on male and female reproductive strategies under thermal stress.

4.2. Effect of Developmental Temperature on Mating Behaviour

We found that developmental temperature significantly affected various aspects of mating behaviour. Males reared at 36 °C were less likely to court than those reared at 27 °C. The reduced probability of courtship initiation in males reared at 36 °C suggests that developmental thermal stress impairs the motivational or physiological threshold for reproductive behaviour. Decreased courtship frequency after heat shock exposure was also observed in *Drosophila*, though these effects were much smaller (Smith et al., 2025; Patton and Krebs, 2001). The intensity of courtship behaviours increases as temperature rises (Rosenthal et al., 2019), thereby increasing the organism's energy expenditure. Previous studies in ectotherms have shown that heat stress increases energy requirements for somatic maintenance (Klepsatel et al, 2016; Harding et al., 2023; Sokolova, 2021). It is likely that in *Gryllodes sigillatus* there is a trade-off in resource allocation between somatic maintenance and reproductive effort, similar to a study in *Gryllus bimaculatus* (Ratz et al., 2024). Consequently, reduced courtship can severely affect population viability by reducing mating frequency. A decreased motivation to court can also impact the intensity of sexual selection, as the cost of finding partners for females can increase, which may lead to females choosing lower quality partners as long as they court.

Furthermore, our study indicated that female body mass had a considerable impact on mating preferences of males. Heavier females were preferred for courtship by the males over lighter ones. The preference or inclination implies that despite the presence of heat stress, there remains some form of sexual selection to maximize reproductive success. Male insects prefer heavier or larger females because they are more likely to be gravid (Bonduriansky and Brooks, 1998; Bonduriansky, 2001) or more fecund (Honěk, 1993). Thus, it is likely that, in *Gryllodes sigillatus,* female body mass serves as an honest signal of reproductive potential, enabling males to assess female quality and choose whom to court.

Contrary to our prediction, our findings reveal that female developmental temperature was the only factor affecting mating latency. Females exposed to high-temperature conditions showed increased mating latency, possibly indicating a shift in the threshold of mate acceptance. Mating latency has been widely studied as a proxy for female mate choice, and a delay could represent a longer assessment period. While rearing temperatures can modulate mate preference and choosiness (Westerman and Monteiro, 2016; Grace and Shaw, 2004), the observed delay may also reflect the high energetic costs of mating for females under thermal stress. This supports the hypothesis that females, as the higher-investing sex, maintain control over mating decisions (Trivers, 1972; Andersson and Iwasa, 1996). Moreover, heat stress may even reinforce this asymmetry by linking the timing of acceptance to female condition. Although mating latency increased, females had a 95.7% probability of mounting the courting males. This could be due to a decreased female mate preference, which occurs in such no-choice experiments (Dougherty and Shuker, 2015). In a natural setting where females can leave the male, this increased latency might translate into total rejection rather than delayed acceptance. While testing for differences in mating latency between females that mated only once and those given repeated opportunities post-hoc, we found no effect of the number of opportunities or development temperature of either sex (ST 9). This suggests that while our experimental constraints may have lowered female choosiness, their underlying selectivity remained robust.

A key feature determining successful mating in this species is the male's transfer of the spermatophore to the female. During mating, alignment between the male and female is critical, enabling the male to transfer his spermatophore into the genital opening of the female, an act that demands precise neuromuscular control (Snell and Killian, 2000). We observed that male development at elevated temperatures negatively affected mating success as the males were frequently unable to transfer their spermatophores. Changes in copulatory behaviours due to heat stress have been previously examined in beetles (Vasudeva et al., 2018). Additionally, heat stress has been shown to alter locomotor activity (Bello et al., 2025), and reduced male motor performance at elevated rearing temperatures may further compromise the physical coordination required for successful spermatophore placement and transfer. Although the developmental temperature of females did not independently affect successful mating, there was an interaction between the developmental temperatures of both sexes. Copulations involving heat-stressed males with heat-stressed females were more successful compared to copulations with control females. Heat exposure might have induced plasticity in females, altering their behaviour during mounting in response to males. Therefore, it is likely that heat-stressed females aligned better with heat-stressed males than control females did. This means that copulation success might be less influenced by the male's performance and more by the physical compatibility between the two individuals, as determined by their thermal histories during development. Nevertheless, further research is needed to identify the precise factors that lead to alignment for successful copulation, and how they are impacted by thermal stress. Our results emphasize the detrimental effects of rising temperatures on mating behaviour, particularly male vulnerability to heat stress, which could drive widespread mating failure, reducing population reproductive output.

Our results indicate that both developmental temperature and body weight are significant determinants of nuptial gift feeding duration in this species. The significant positive effect of male weight on feeding duration likely supports the hypothesis that larger males provide higher-quality gifts, which may extend ampulla attachment and enhance fertilization success (Fedorka and Mousseau, 2002). Additionally, larger males may guard females for longer durations, which has been shown to directly extend female feeding time on the nuptial gift and enhance ampulla retention (Haneke-Reinders et al., 2020; Rizvi and Reinhold, 2026). However, due to the mixed evidence on the correlation of mass and mate-guarding duration, these possibilities can only be speculated at this stage. 36°C-reared females fed longer despite their greater mass, likely reflecting heat-induced nutritional deficits (lower lipid reserves despite larger size; Enriquez & Visser 2023) and impaired digestive efficiency (enzyme inhibition; Grčić et al. 2023). This compensatory feeding behaviour addresses the persistent metabolic costs of developmental stress.

4.3. Effect of Developmental Temperature on Reproductive Output

Our results show that developmental heat stress significantly reduced female fecundity, consistent with broader patterns of thermal trade-offs in ectotherms. While high temperatures often accelerate metabolic processes, they can also impose physiological costs, such as reduced allocation to reproductive tissue (Siegle et al., 2022; Gremion et al., 2025). The positive relationship we observed between female mass and egg production is well-documented across numerous insect species; larger females generally possess greater lipid and protein reserves, allowing them to translate superior nutritional status into higher fecundity (Bateman et al., 2001; Lease and Wolf, 2011). However, in our case, although females reared at 36°C were heavier, they paradoxically exhibited lower fecundity over the two-week observation period. This finding suggests a significant physiological trade-off: while high developmental temperatures may promote increased body mass, they may also impair reproductive output. This could occur by shifting energy away from egg production toward somatic maintenance or by altering the maturation rate of oocytes (Awde et al., 2023; Schou et al., 2021).

There was also a marked decline in female fertility under heat-stress conditions. Hatching success for eggs produced by heat stressed females during both the first and second weeks after mating, was lower. This persistent reduction suggests that developmental heat stress can induce long-lasting physiological damage that cannot be recovered during the adult stage. Effects of heat stress on mosquito and *Drosophila* fertility (Pekľanská et al., 2025; Kirk Green et al., 2019) have been previously observed, with heat-stressed females exhibiting reduced fertility. A low hatching rate could be attributed to changes in the structure and function of sperm-storing organs (Farrow et al., 2021), resulting in reduced sperm numbers or malfunctioning of the biochemical processes that sustain their vitality. Another possible factor leading to reduced fertility is maternal influence on oocyte quality, whereby elevated developmental temperature induces apoptosis in the germline. Such effects of developmental heat stress have been observed in *Drosophila melanogaster* (Gandara and Barbosa, 2022), where females reared at warm temperatures exhibit impaired oocyte quality and increased germline cyst death and in pufferfish (Lee et al., 2009), where high temperature treatment during gonadal development led to complete germ cell degeneration.

Through our experimental design, we were interested in disentangling sex-specific effects on fitness-related traits, however the high rate of unsuccessful copulations involving the heat-stressed males resulted in insufficient data to determine any paternal effects (98% and 76% of the matings failed between 36°C males x 27°C females and 36°C males x 36°C females, respectively). Given that male sperm quality is a critical determinant of reproductive success (Wang and Gunderson, 2022), examining the independent effects of male developmental temperature on sperm function and hatching success represents an important and necessary extension of this work. Thermally induced reductions in male fertilisation capacity would directly diminish male fitness by reducing paternity and simultaneously impose indirect fitness costs on females that invest energetic resources into mating and egg production without the benefit of successful fertilisation, thereby affecting overall population viability.

4.4. Effect of Environmental Temperature on Mating Behaviour

The mating behavioural repertoire of heat-stressed individuals was largely robust to environmental thermal variation except the number of times a pair attempted to mate and the nuptial gift feeding time by females. The frequency of mating attempts increased by 88.42% when mating was carried out under heat-stress conditions. While locomotion and activity levels in insects typically rise with temperature (Hannigan et al., 2023; Suverkropp et al., 2001; Taylor, 1963), this heat-induced hyperactivity may impair the coordination required for successful copulation, necessitating repeated mating attempts. Furthermore, elevated temperatures increase metabolic rates (Riemer et al., 2018), which may have led to faster feeding under heat stress as females attempt to meet the greater energetic demands of a high-temperature environment. Consistent with our previous results (see 4.2) male body mass also played a significant role as females mated to heavier males fed longer.

4.5. Conclusion

To summarise, our study provides evidence that both male and female developmental temperatures modulate life-history traits, morphology, mating behaviours, and reproductive output. Such studies are becoming increasingly important for disentangling sex-specific effects on reproduction, as the two sexes are subject to different selective pressures and physiological constraints that shape their distinct responses to environmental stress. As global temperatures continue to rise, understanding how heat stress experienced during development translates into impaired adult reproductive function becomes increasingly urgent, particularly for ectotherms whose life-history traits and mating behaviours are inextricably linked to their thermal environment. Our findings, therefore, contribute to a growing body of evidence that climate warming poses a significant threat to the reproductive integrity of ectotherm populations, shaping reproductive success, population fitness, and the evolutionary dynamics of sexual selection.

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Author Contributions

TR: Conceptualisation, Methodology, Software, Formal Analysis, Investigation, Project Administration, Visualisation (supporting) Supervision (lead), Writing - Review and Editing (lead) **DS:** Conceptualisation, Data Curation, Methodology, Software, Formal Analysis, Investigation, Project Administration, Visualisation (lead), Writing - Original Draft, Writing - Review and Editing (supporting) **KR:** Resources, Funding Acquisition, Supervision (supporting), Writing - Review and Editing (supporting)

Conflict of Interest Declaration

The authors declare no competing interests.

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SUPPLEMENTARY MATERIAL

***ST 1**: Summary of Firth's Penalized Cox Proportional Hazards Regression model for the effect of temperature and sex on development rate. 95% CI and p-values calculated by Profile Likelihood.*

Variable	**Coefficient (β)**	**HR (eβ)**	**95% CI**	**p - value**
Temperature (36 °C)	7.556	1911.69	[258.55, 244,893.6]	< 0.001
Sex (Male)	- 0.333	0.716	[0.569, 0.902]	0.005

***ST 2:** Summary of Linear model for the effect of temperature, sex, and their interaction on body mass, and post-hoc analysis of differences within sex.*

Section	**Comparison / Variable**	**Estimate**	**Std. Error**	**t-ratio**	**p-value**
Model Coefficients	(Intercept: Female 27°C)	0.350	0.007	49.31	< 0.001
	Temperature (36°C)	+0.078	0.010	7.83	< 0.001
	Sex (Male)	-0.089	0.010	-9.13	< 0.001
	Interaction (Temperature × Sex)	**-0.074**	**0.014**	**-5.41**	**< 0.001**
Post-Hoc (Within Sex)	**Females:** 27°C vs 36°C	**-0.078**	0.009	-7.83	**< 0.001**
	Males: 27°C vs 36°C	**-0.003**	0.009	-0.37	**0.710**

***ST 3:** Summary of posterior estimates from Bayesian Generalized Linear Mixed model for the effect of male rearing temperature, female rearing temperature, and their interaction on the probability of male initiating courtship.*

Predictor	**Estimate (Mean)**	**Est. Error**	**Lower 95% CI**	**Upper 95% CI**	**Rhat**

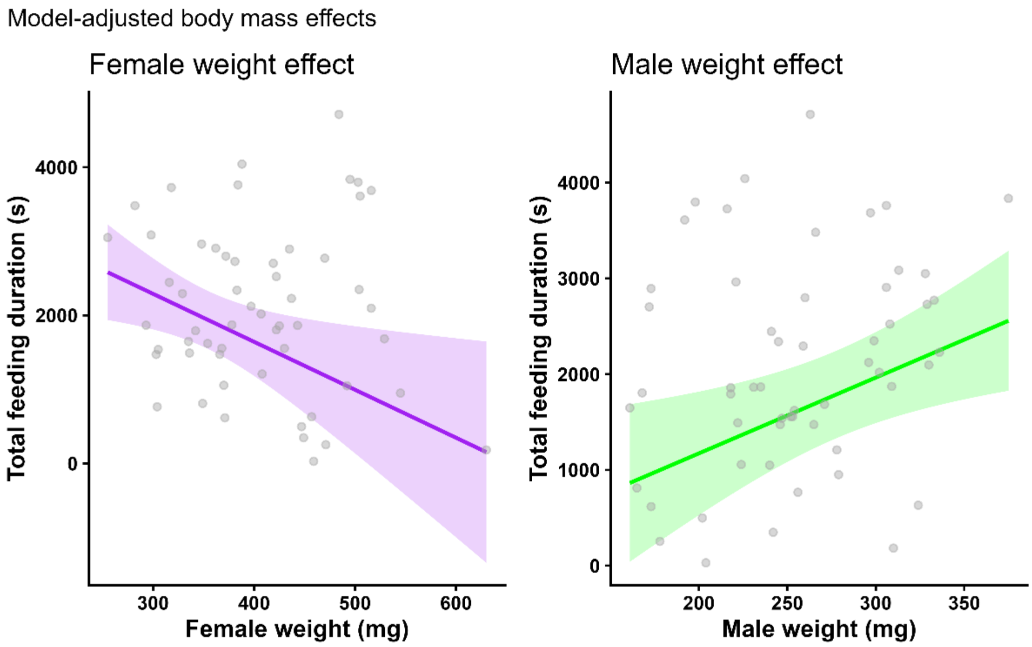
Intercept	2.65	0.74	1.34	4.23	1.00
Female Temperature (36°C)	-0.63	1.01	-2.65	1.36	1.00
Male Temperature (36°C)	**-4.80**	**1.03**	**-7.06**	**-2.99**	**1.00**
Female Weight (z)	**0.45**	**0.21**	**0.04**	**0.87**	**1.00**
Male Weight (z)	-0.47	0.30	-1.08	0.09	1.00
Female Temperature × Male Temperature	2.17	1.26	-0.23	4.74	1.00

ST 4: *Summary of Linear Mixed Effects model for the effect of male rearing temperature, female rearing temperature, and their interaction on log-transformed mating latency.*

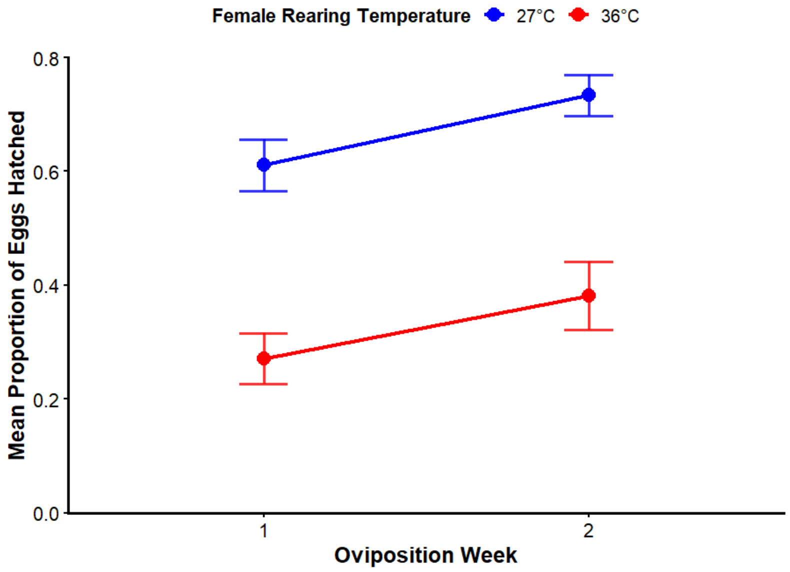
Type	**Predictor**	**Estimate**	**Std. Error**	**df**	**t value**	**p-value**
Fixed Effects	(Intercept)	1.587	0.215	96.88	7.37	< 0.001
	Male Temperature (36°C)	0.297	0.326	92.46	0.91	0.364
	Female Temperature (36°C)	**0.990**	**0.357**	**100.79**	**2.77**	**0.007**
	Male Weight (z)	-0.153	0.103	177.38	-1.48	0.141
	Female Weight (z)	-0.056	0.132	108.75	-0.42	0.674
	Male Temperature × Female Temperature	-0.054	0.451	95.16	-0.12	0.905
Random Effects	**Groups**	**Variance**	**Std. Dev.**			
	Female ID	0.3026	0.5501			
	Male ID	0.0000	0.0000			
	Residual	1.6062	1.2673			

ST 5: *Summary of Generalized Linear Mixed model for the effect of male rearing temperature, female rearing temperature, and their interaction on mating success.*

Type	**Predictor**	**Estimate (Log-Odds)**	**Std. Error**	**z value**	**p-value**
Fixed Effects	(Intercept)	1.052	0.533	1.973	0.048
	Male Temperature (36°C)	**-5.256**	**1.363**	**-3.858**	**< 0.001**
	Female Temperature (36°C)	0.071	0.674	0.106	0.916
	Male Weight (z)	0.061	0.222	0.276	0.782
	Female Weight (z)	0.209	0.261	0.802	0.422
	Male Temperature × Female Temperature	**2.665**	**1.324**	**2.013**	**0.044**
Random Effects	**Groups**	**Variance**	**Std. Dev.**		
	Male ID	1.001	1.000		
	Female ID	< 0.001	< 0.001		



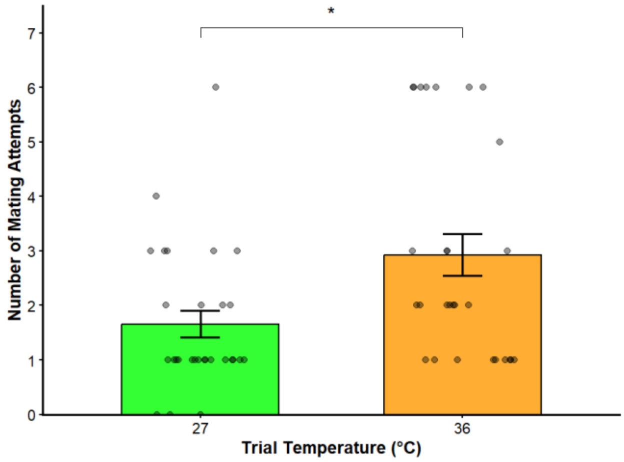
***S 1:** Model-adjusted relationships between body mass and total feeding duration. The left panel shows the effect of female weight, and the right panel shows the effect of male weight. Grey points indicate individual observations, coloured lines represent fitted linear model predictions, and shaded bands show 95% confidence intervals. The models were adjusted for the remaining covariates in the full linear model.*



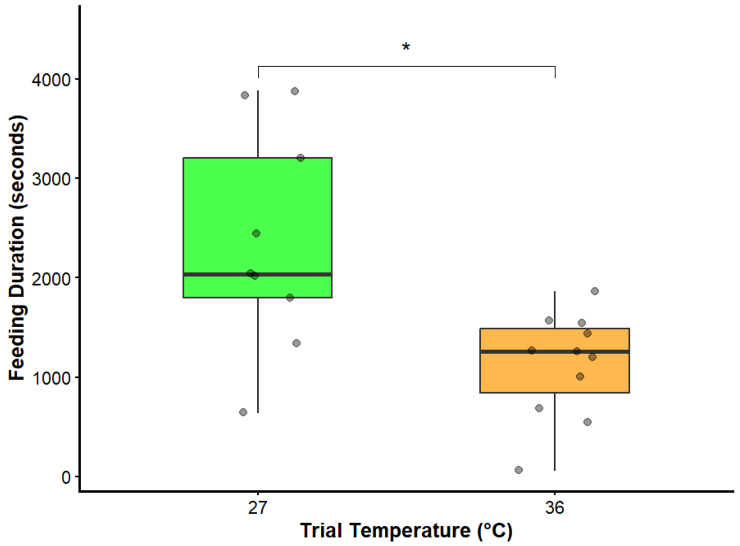
***S 2:** Effect of female developmental temperature on fertility (week-wise). Eggs laid by females reared at 27 °C in the first- and second-week post-mating showed greater success of hatching than eggs laid by females reared at 36 °C. Vertical error bars represent the standard error (±SE), while points represent the mean.*

ST 6: *Summary of generalized linear mixed models for hatching success of eggs laid in the first week, second week post-mating, and overall.*

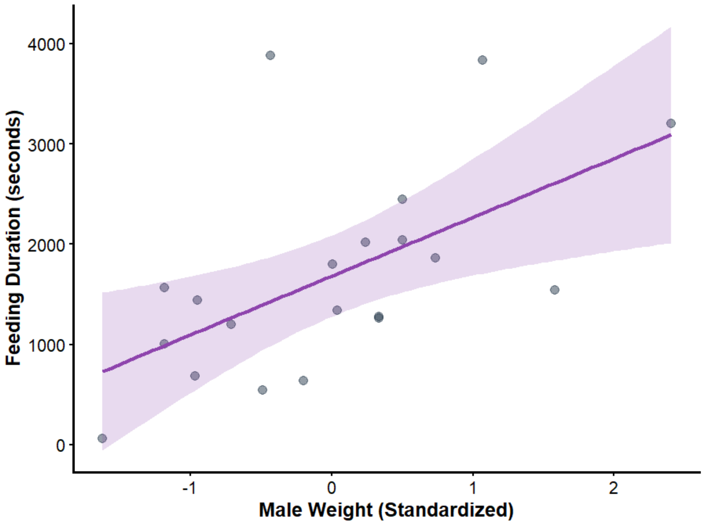
Model (Time)	**Predictor**	**Estimate (β)**	**Std. Error**	**z-value**	**p-value**	**Odds Ratio [95%CI]**
Week 1	Intercept	0.236	0.245	0.96	0.335	1.27 [0.78, 2.05]
	Temperature (36°C)	**-1.048**	**0.406**	**-2.58**	**0.009**	**0.35 [0.16, 0.77]**
	Female Weight	-0.190	0.207	-0.92	0.359	0.83 [0.55, 1.24]
Week 2	Intercept	0.842	0.258	3.26	0.001	2.32 [1.40, 3.84]
	Temperature (36°C)	**-1.321**	**0.425**	**-3.11**	**0.002**	**0.27 [0.12, 0.61]**
	Female Weight	0.006	0.199	0.03	0.978	1.01 [0.68, 1.49]
Overall	Intercept	0.428	0.201	2.13	0.034	1.53 [1.03, 2.28]
	Temperature (36°C)	**-1.226**	**0.325**	**-3.77**	**<0.001**	**0.29 [0.15, 0.55]**
	Female Weight	-0.311	0.170	-1.83	0.067	0.73 [0.52, 1.02]



S 3: *Effect of trial temperature on number of mating attempts. Individuals mating at 36 °C show a greater number of mating attempts than those mating at 27 °C. Solid bars represent the mean number of mating attempts, while vertical error bars indicate standard error (±SE).*



S 4: *Effect of trial temperature on feeding duration of nuptial gift. At a higher ambient temperature of 36 °C, females fed on the nuptial gift much faster than at 27 °C. Horizontal bars indicate the median feeding duration, and boxes indicate the interquartile range.*



S 5: *Effect of male weight on the feeding duration of the nuptial gift by females. Females mated with heavier males show an increase in feeding duration compared to those mated with lighter males.*

ST 7: *Summary of Negative Binomial Generalized Linear Mixed Model for the effect of trial temperature on the number of mating attempts*

Type	**Predictor**	**Estimate (Log-Count)**	**Std. Error**	**z value**	**p-value**
Fixed Effects	(Intercept)	0.412	0.183	2.246	0.025

	Trial Temperature (36°C)	**0.634**	**0.248**	**2.555**	**0.011**
	Male Weight (z)	0.118	0.111	1.065	0.287
	Female Weight (z)	0.009	0.132	0.069	0.945
Random Effects	**Groups**	**Variance**	**Std. Dev.**		
	Female ID	0.0977	0.3125		
	Male ID	< 0.001	< 0.001		

ST 8: *Summary of Linear Mixed-Effects Model for the effect of trial temperature on the feeding duration of nuptial gift*

Type	**Predictor**	**Estimate**	**Std. Error**	**df**	**t value**	**p-value**
Fixed Effects	(Intercept)	2274.65	314.21	14.78	7.239	< 0.001
	Trial Temperature (36°C)	**-1098.01**	**452.85**	**15.18**	**-2.425**	**0.028**
	Male Weight (z)	**536.39**	**230.32**	**15.80**	**2.329**	**0.034**
	Female Weight (z)	-212.56	142.97	2.91	-1.487	0.236
Random Effects	**Groups**	**Variance**	**Std. Dev.**			
	Male ID	623,700	789.70			
	Female ID	< 0.001	< 0.001			
	Residual	59,040	243.00			

ST 9: *Summary of Linear mixed effects model for the effect of male rearing temperature, female rearing temperature, their interaction, and female experience on log-transformed mating latency.*

Type	**Predictor**	**Estimate**	**Std. Error**	**df**	**t value**	**p-value**
Fixed Effects	(Intercept)	1.972	0.258	73.13	7.634	< 0.001
	Male Temperature (36°C)	0.193	0.366	76.89	0.527	0.600
	Female Temperature (36°C)	0.684	0.359	78.90	1.905	0.060
	First Success (Yes)	-0.414	0.297	133.05	-1.395	0.165
	Male Weight (z)	**-0.243**	**0.110**	**153.14**	**-2.207**	**0.029**
	Female Weight (z)	-0.138	0.133	90.63	-1.036	0.303
	Female Temperature × Male Temperature	0.107	0.465	77.11	0.229	0.819
Random Effects	**Groups**	**Variance**	**Std. Dev.**			
	Female ID	0.1712	0.4138			
	Male ID	0.0000	0.0000			