

1 Effects of temperature on the development of *Heliconius* 2 *erato* butterflies

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8

9 Abstract

- 10 1. Anthropogenic climate change is thought to present a significant threat to biodiversity, in
11 particular to tropical ectotherms, and the effects of long-term developmental heat stress on
12 this group have received relatively little research attention.
- 13 2. Here we study the effects of experimentally raising developmental temperatures in a tropical
14 butterfly. We measured survival, development time, adult body mass, and wing size of a
15 neotropical butterfly, *Heliconius erato demophoon*, across three temperature treatments.
- 16 3. Egg survival was lower in the hotter treatments, with 83%, 73%, and 49% of eggs eclosing in
17 the 20-30°C, 23-33°C, and 26-36°C treatments, respectively. Larval survival was five times
18 lower in the 26-36°C treatment (4%) compared to the 20-30°C treatment (22%), and we did
19 not detect differences in pupal survival across treatments due to high mortality in earlier
20 stages.
- 21 4. Adults in the 20-30°C treatment had a lower body mass and larvae had a lower growth rate
22 compared to the intermediate 23-33°C treatment, but were heavier than the few surviving
23 adults in the 26-36°C treatment. Females were heavier and grew faster as larvae than males
24 in the 23-33°C treatment, but there was no associated increase in wing size.

25 5. In summary, high developmental temperatures are particularly lethal for eggs and less so for
26 larvae, and also affect adult morphology. This highlights the importance of understanding the
27 effects of temperature variation across ontogeny in tropical ectotherms.

28 Keywords: Heliconius, heat stress, developmental temperature, climate change, Lepidoptera

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30

31 Introduction

32 Environmental temperature is one of the most critical ecological parameters for ectothermic
33 species, as they have limited ability to adjust their body temperature (Sunday *et al.*, 2011). Thus, both
34 prevailing weather and long-term climate change directly impact insects, and their capacity to cope
35 with varying temperatures is critical for species survival and dispersal. Exposure to a high temperature
36 typically reduces individual fitness and ultimately causes death through protein denaturation,
37 disruption of membrane structure, and desiccation (Klockmann *et al.*, 2017b). Furthermore, heat
38 stress may lead to long-term life-history trade-offs in those survivors, restricting future reproductive
39 success (Jourdan *et al.*, 2019). Under current global warming projections, high temperatures and
40 extreme climate events will be more frequently encountered in the future, which may strongly impact
41 biodiversity (IPCC 2021).

42 Although half of known animal species are tropical ectotherms, our knowledge about how
43 well they can withstand high temperatures remains limited (García-Robledo *et al.*, 2016; Sheldon,
44 2019). There are many studies on the effects of heat stress on the development of animals
45 (Piyaphongkul *et al.*, 2012), but fewer have focused on tropical insects. Furthermore, the majority of
46 these studies have focussed on adults, thus, much less is known about the impact of thermal stress
47 throughout development (Klockmann *et al.*, 2017b). Tropical insects are predicted to be especially
48 vulnerable to elevated temperatures (Janzen, 1967). Since environmental temperatures in the tropics
49 are largely stable throughout the year, this could potentially lead to narrow thermal tolerance in
50 tropical species (Polato *et al.*, 2018; Sheldon, 2019). As such, tropical ectotherms are likely to be living

51 near their upper-temperature limits already and may not be able to cope with a large increase in
52 developmental temperatures (Deutsch *et al.*, 2008; Fischer *et al.*, 2014). Thus, it is important to
53 determine the ability of tropical ectotherms to overcome the physiological constraints posed by
54 increasing temperatures (Piyaphongkul *et al.*, 2012).

55 Thermal stress experienced by juveniles may further affect adults (“carry-over effects”;
56 Klockmann *et al.*, 2017b). Juveniles surviving heat stress may have reduced fitness as adults, and
57 could influence life-history trade-offs (Jourdan *et al.*, 2019). Under elevated temperatures, there may
58 be a trade-off in phenology and morphology, resulting in shorter development time and emergence
59 at a lower adult body size (Chown & Gaston, 2010; Fischer *et al.*, 2014). Adult body size is often a
60 predictor of lifespan, competitiveness, and reproductive success, possibly impacting population
61 viability (Fischer *et al.*, 2004; Kingsolver & Huey, 2008). Therefore, carry-over effects from juvenile
62 heat stress could severely impact adult fitness. Improving our understanding of tropical insect
63 responses to global warming will necessitate considering the effects of heat stress on both survival
64 and other fitness traits throughout development (Klockmann *et al.*, 2017b).

65 This study investigates the effects of increased temperatures on survival and development in
66 a Neotropical butterfly *Heliconius erato demophoon*. *H. erato* is a pollen-feeding butterfly ranging
67 from southern Texas to northern Paraguay and often inhabits fringes of tropical rainforests (Turner,
68 1971). Previous studies have shown plasticity in heat tolerance when butterflies from different
69 elevations were reared in a common-garden environment, with butterflies from different populations
70 showing similar heat tolerances despite strong differences in the wild (Montejo-Kovacevich *et al.*,
71 2020). Here we test the vulnerability of each juvenile stage to sustained heat stress by testing the
72 survival and growth rate of eggs, larvae, and pupae. We then investigate the effects of elevated
73 temperatures on other traits in the surviving adults, including adult mass and wing development.

74 Materials and Methods

75 Study system

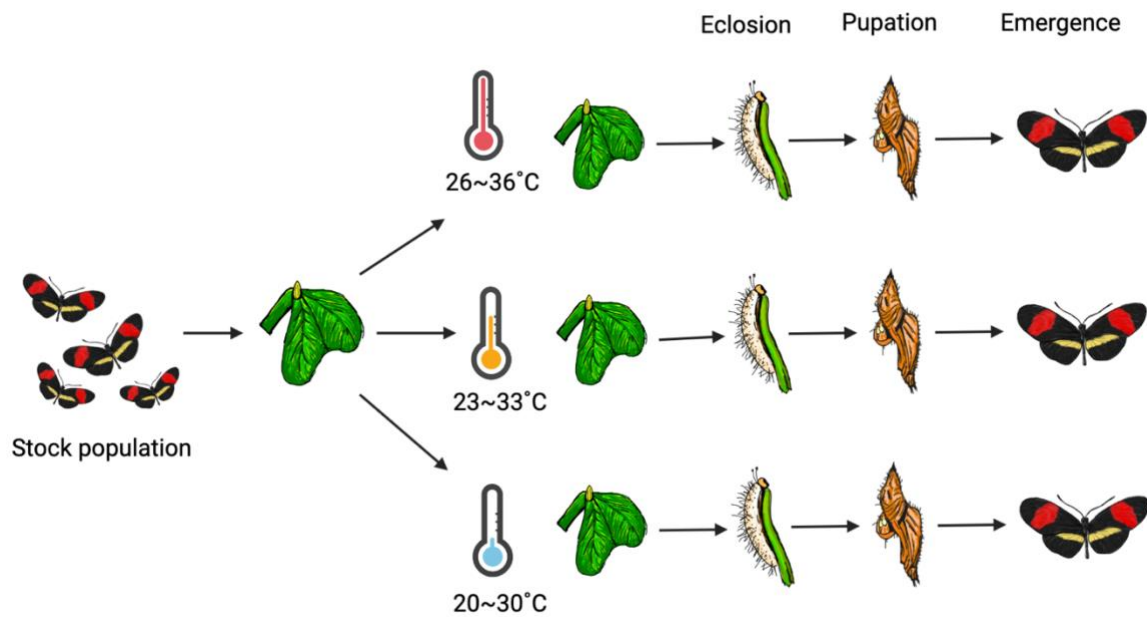
76 We used an established laboratory stock population at the Madingley rearing facility,
77 University of Cambridge, UK, that was started in 2017 with *Heliconius erato demophoon* butterflies
78 from Panama. The larvae of the stock population were reared at 25°C, 75% relative humidity, and a
79 photoperiod of L12:D12 within a single temperature-, light-, and humidity-controlled CT room. The
80 adults were kept in the insectaries, which experienced variable diurnal temperature changes. The
81 larvae were fed with tips of *Passiflora biflora*, and adults were fed with pollen from *Lantana camara*
82 and supplemented with protein-incorporated sugar solution.

83

84 Experimental design

85 Eggs were collected from dozens of females in the stock population in the summer of 2021.
86 Since the stock populations had been reared and bred together for multiple generations, effects due
87 to genetic differences between parents were considered negligible, and thus, we did not track
88 pedigrees in this experiment. However, each egg was tracked individually through development.

89 The host plants *P. biflora* were removed from the cages with adults 24-48 hours before
90 collecting eggs, to encourage females to lay when the host plants were reintroduced. Approximately
91 20 *H. e. demophoon* females were allowed to oviposit on a small *P. biflora* plant for a three-hour
92 session on three consecutive days, from which the eggs were collected hourly, and time was noted.
93 Three eggs were placed per small plastic pot. Pots were randomly placed among three treatment
94 groups within 2 hours of laying (Figure 1). Climate chambers were heated up to the target temperature
95 before the transfer of pots, and the light: dark, and temperature cycles were 12h:12h across cabinets.
96 The 20-30°C temperature (i.e., 12h of 20°C followed by 12h of 30°C, also referred to as the cold
97 treatment) was used as a control for the comparison, with the same mean temperature as the normal
98 rearing temperature of the stock population, i.e. 25°C. The 23-33°C temperature (also referred to as



99

100 Figure 1. Experimental design. The stock population was allowed to oviposit on the host plant,
101 *Passiflora biflora*, and the eggs were randomly separated into three temperature treatment groups
102 (20-30°C, 23-33°C, or 26-36°C). The time of eclosion, pupation, and emergence were tracked, as well
103 as individual survival and mass.

104

105 the intermediate treatment) used is within the range of temperature experienced by *H. e. demophoon*
106 in some locations of its natural habitat, and 26-36°C (also referred to as the hot treatment) represents
107 temperatures only experienced occasionally in forest canopies in the Equator (Montejo-Kovacevich *et*
108 *al.*, 2020) but that could become common in degraded lowland habitats in the tropics (Luber &
109 McGeehin, 2008).

110 Survival rates and development times for eggs, larvae, and pupae were measured (Figure 1).

111 Egg eclosions were checked three times a day at 10 am, 1 pm, and 4 pm for seven days after laying
112 and time was noted. Eggs were considered dead if no larvae had emerged after seven days. The larvae
113 from each temperature group were transferred into plastic boxes lined with moist tissue and *P. biflora*
114 with three to five larvae per box and survival was checked every two days. Pupation and emergence
115 dates were recorded to obtain larval and pupal development time. Pupae were weighed between 2

116 and 4 days after pupation. Each pupa was hung in an individual, labelled pot once weighed. After
117 emergence, butterfly wings were carefully removed from the thorax with forceps to best maintain the
118 whole structure. Adult body mass was measured after wing removal, and bodies were stored in pure
119 ethanol at -20°C for future studies.

120

121 Wing image analysis

122 Wing size was obtained from images of the detached wings of the individuals that reached
123 adulthood (n=78). Detached wings were photographed dorsally and ventrally with a DSLR camera with
124 a 100 mm macro lens in standardised conditions. Any damaged or folded specimens were excluded
125 from the analysis. A custom script for Fiji (Schindelin *et al.*, 2012), which automatically crops, extracts
126 the forewings, and performs particle size analysis, was used to obtain wing measurements from the
127 images (Montejo-Kovacevich *et al.*, 2019a). We obtained an average wing area between the forewings
128 (where possible, in mm², hereafter “size”) since butterflies predominantly use their forewings for flight
129 (Le Roy *et al.*, 2019).

130

131 Statistical analysis

132 We analysed (1) the survival rates of eggs/larvae/pupae as the percentage of
133 eclosion/pupation/emergence per treatment group, respectively, (2) development time across
134 treatments, (3) pupal mass and adult body mass per treatment group and sexes, and (4) wing size and
135 wing loading between treatment groups and sexes. Pairwise t-tests were performed for the means of
136 each treatment group. Bonferroni adjustments were performed after chi-squared tests if the group
137 number was more than two. All statistical analyses were run in R V1.3.1093 (R Development Core
138 Team 2011), and graphics were generated with the package ggplot2 (Ginestet, 2011).

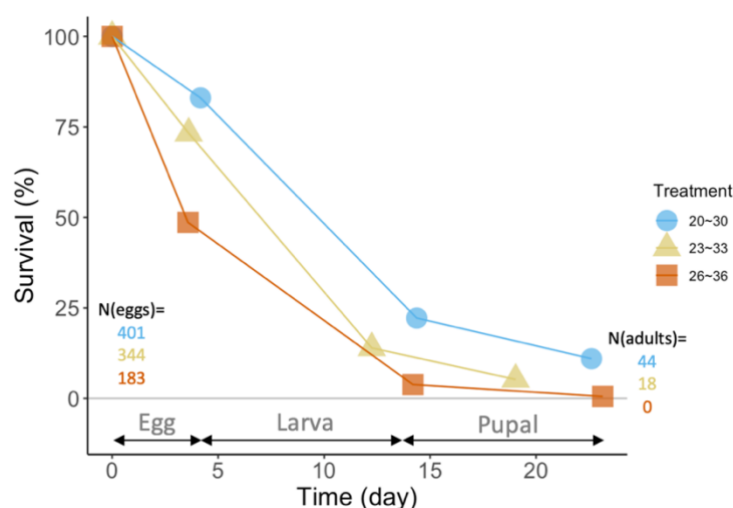
139 Results

140 Survival and development time

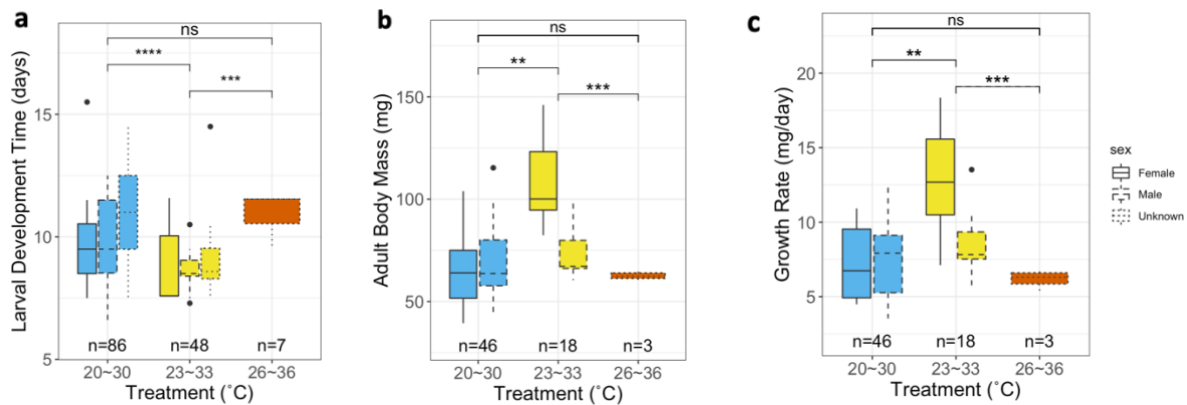
141 The survival rate of all stages decreased under heat stress (Figure 2). Egg and larval survival
142 were both affected by heat stress ($X^2(2, N = 928) = 74.95, p < 0.0001$, and $X^2(2, N = 633) = 16.01, p <$
143 0.001 , respectively). Post hoc pairwise comparisons of survival revealed that egg survival was lower in
144 the two hotter treatments (egg survival was 83.0%, 73.3%, and 48.6%, respectively) whereas larval
145 survival was only significantly lower in the 26-36°C treatment compared to the 20-30°C treatment
146 (larval survival was 22.2%, 14.0%, and 3.8%, respectively). We did not detect differences in pupal
147 survival across treatments, but sample sizes were lower due to mortality in earlier stages ($X^2(2, N =$
148 $144) = 4.40, p = 0.11$).

149 Timing of larval death was not correlated with rearing temperature. However, individuals that
150 died as pupae in the 20-30°C treatment took around 30 hours longer to develop as larvae compared
151 to those that successfully emerged as adults in the same treatment ($t(41) = 2.55, p = 0.014$, and $t(53)$
152 $= 2.87, p = 0.0059$ larval development time of females/males that reached adulthood compared to
153 that of those that died as pupae, classed as unknown sex in Fig 3A treatment 20-30°C, respectively).

154 Figure 2. Percentage of individuals surviving during egg, larval, and pupal stages in three temperature



155 treatments (blue = 20-30°C, yellow = 23-33°C, and red = 26-36°C).



156 Figure 3. Growth and development across treatments and sexes: (a) larval development time, (b) adult
 157 body mass (mg), and (c) growth rate measured as mass gain (mg) per day. Blue, yellow and orange
 158 bars represent 20-30°C, 23-33°C and 26-36°C treatment, respectively. Solid lines are females and
 159 dashed lines are males. Top values showing significant levels of pairwise t-tests between each
 160 treatment group ($\bullet < 0.1$, $* < 0.05$, $** < 0.01$, $*** < 0.001$). Individuals that died at the pupal stage
 161 were not sexed ('Unknown' sex category).

162

163 Overall development time was fastest in the intermediate treatment (19.0 ± 1.4 days) and
 164 similar in the cold and hot treatments (22.6 ± 1.9 days and 23.1 ± 0.6 days, respectively). There was
 165 no significant difference in development times between sex in each treatment group ($p = 0.70$).

166

167 Mass and growth rate

168 Adults were heaviest in the intermediate treatment (for 20-30°C and 23-33°C, $t(24) = 2.87$, p
 169 < 0.01 ; 23-33°C and 26-36°C, $t(18) = 4.04$, $p < 0.001$), but the cold and hot treatments yielded adults
 170 with similar body mass ($t(21) = 1.89$, $p = 0.07$, Figure 3B). Nevertheless, when comparing adults of the
 171 same sex between treatments, females in the intermediate treatment were heavier than females in
 172 the cold treatment ($t(8) = 4.21$, $p < 0.01$), whilst males in the cold and intermediate groups did not
 173 significantly differ in weight. Further, females in the intermediate group were significantly heavier
 174 than males in the same treatment (t-test between sexes in 23-33°C, $t(7) = 3.70$, $p < 0.01$). Thus, the

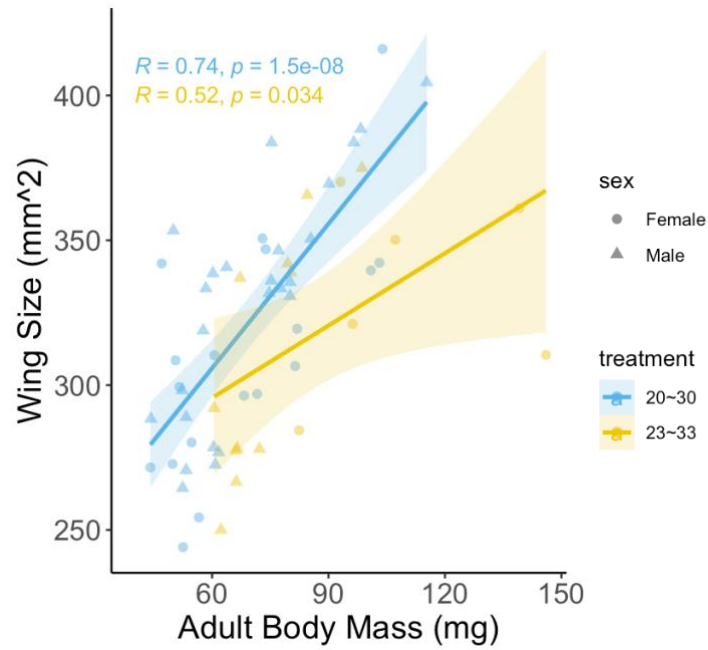
175 difference in mean body mass between cold and intermediate treatment was driven by heavier
176 females in the intermediate temperatures. Pupal weight was similar between the cold and
177 intermediate groups but decreased significantly at 26-36°C (for 20-30°C and 26-36°C, $t(16) = 3.06$, $p <$
178 0.01 , and 23-33°C and 26-36°C, $t(20) = 4.28$, $p < 0.001$).

179 Growth rate, which is the ratio between adult body mass and larval development time (since
180 growth only occurs at the larval stage), was highest at 23-33°C and decreased at 26-36°C compared to
181 the 20-30°C treatment (for 20-30°C and 23-33°C, $t(22) = 3.21$, $p < 0.01$, and 23-33°C and 26-36°C, $t(17)$
182 $= 4.26$, $p < 0.001$, Figure 3C). However, only females from the 23-33°C had an elevated growth rate
183 compared to the females from the 20-30°C treatment ($t(17) = 4.26$, $p < 0.001$), not the males. Since
184 there was no difference between development times, females in higher temperatures grew both
185 faster and heavier. In summary, a small increase in temperature led to a faster growth rate, but the
186 growth rate dropped when the temperature was too high.

187

188 Wing size and loading

189 There was no difference in wing size between temperature treatments or sexes ($R^2_{LM} = -0.02$,
190 $F(2, 59) = 0.42$, $p = 0.66$; Figure 4). The hot treatment was excluded from the comparison as most
191 individuals in this treatment did not reach adulthood. Temperature treatment and sex were both
192 predictors of wing loading, which is the ratio between the adult body mass and wing size ($R^2_{LM} = 0.27$,
193 $F(2, 57) = 12.15$, $p < 0.0001$). Females in the 23-33°C treatment had a greater wing loading than males
194 in the same group ($t(5) = 2.78$, $p = 0.04$). These differences in wing loading were likely driven by the
195 higher adult body mass in the warmer treatment since there was no difference in wing size.



196

197 Figure 4. Adult wing size and body mass allometry. Wing analyses between treatment groups (blue =

198 20-30°C, yellow = 23-33°C). Pearson correlation coefficients and p-values are shown for the regression

199 lines per treatment.

200

201 Discussion

202 Insects have developed a variety of adaptations to endure temperature variation (Overgaard
203 *et al.*, 2008), yet there are temperature thresholds beyond which species cannot live. This study
204 revealed that a 3°C temperature increase to 23-33°C led to higher egg mortality and a 6°C temperature
205 increase to 26-36°C led to both higher egg and larval mortality compared to developing at 20-30°C.
206 The few survivors of 26-36°C had a significant decline in adult body mass, growth rate, and wing
207 loading. In contrast, the slight elevation from 20-30°C to 23-33°C increased adult body mass and
208 growth rate, but the fitness consequences of these trait shifts were not assessed.

209

210 Temperature affects survival and development

211 In line with earlier studies, we found strong adverse effects of high temperature on both egg-
212 hatching success and larval survival (Piyaphongkul *et al.*, 2012; Kingsolver *et al.*, 2015; Klockmann *et*
213 *al.*, 2017a). These detrimental effects could be explained by, for instance, denaturation of proteins,
214 disruption of membrane structure, or desiccation (Klose & Robertson, 2004; Chown & Terblanche,
215 2006; Potter *et al.*, 2009). The *H. e. demophoon* larvae here studied seems to be well equipped to bear
216 temperatures slightly above the normal rearing temperature (25 °C) of the stock, as there were no
217 differences in larval and pupal mortality between the 20-30°C and 23-33°C treatments.

218 Furthermore, it is remarkable that some individuals survived cycles of 12 hours at 36°C in the
219 26-36C treatment, as individuals of the same species have been shown to get knocked down after only
220 15.9 minutes when exposed to temperatures between 39 and 41°C (Montejo-Kovacevich *et al.*, 2020).
221 Many studies have looked at the maximum temperature organisms can endure (critical thermal
222 maximum) or perform short exposures to high temperatures and measured the time until they are
223 knocked down (Bowler & Terblanche, 2008; Ju *et al.*, 2014; Nandi & Chakraborty, 2015). Our findings
224 suggest that responses to short exposures may not correlate so well to long exposures. In the wild,
225 short exposures may be relevant to complex habitats such as tropical forests where microclimates are

226 buffering against heat stress, acting as refugia (Scheffers *et al.*, 2014). But for other more open or
227 degraded habitats, temperature increases may be more homogenous throughout space and time of
228 the day (De Frenne *et al.*, 2019; Montejo-Kovacevich *et al.*, 2020). Therefore, testing different
229 exposure times and temperatures for different habitat types would be interesting for future studies.

230 The ability to survive in hot conditions changes through development, with eggs having the
231 lowest survival, followed by larvae. Different hypotheses as to why heat tolerance varies through
232 development have been proposed. First, individuals with a larger size may have higher survival under
233 heat stress (Kingsolver & Huey, 2008; Klockmann *et al.*, 2017a). Klockmann *et al.* (2017b), for example,
234 found that survival was higher for larger caterpillars of *Bicyclus anynana*. Nonetheless, we did not find
235 size-dependency in heat tolerance within larval development as the time of larval death did not differ
236 between the treatment groups. Second, the enhanced survival of larvae compared to eggs may be
237 attributed to behavioural responsiveness. Since desiccation is an important factor contributing to the
238 high mortality under heat stress, the consumption of food by the larvae may allow them to acquire
239 water and energy which are essential for evaporative cooling to prevent desiccation (Klockmann *et al.*,
240 2017a). Finally, habitat use by wild butterflies may further explain why eggs are sensitive to high
241 temperatures. Eggs may not be under strong selection pressure to evolve heat tolerance in the wild if
242 they inhabit the understory and near the moist leaves, which can provide microclimate buffering
243 against heating (Madigosky, 2004). The understory of tropical forests inhabited by *Heliconius* in
244 Ecuador has, on average, 1.75°C cooler daily maximum temperature than the sub-canopy (Montejo-
245 Kovacevich *et al.*, 2020). The absence of such refugia in our experiment, with only a few leaves and/or
246 stems of the plant in each pot, may have exacerbated the heat stress suffered by the eggs. Overall, our
247 findings are broadly in line with similar experiments on *Bicyclus anynana* butterflies and highlight the
248 importance of preserving habitat complexity for buffering against heat stress in vulnerable and
249 immobile early life stages of tropical ectotherms.

250 Our results showed that adult body mass was higher at 23-33°C relative to the 20-30°C
251 treatment, but lower at 26-36 °C. Since temperature is known to have a major influence on various

252 developmental processes in ectotherms (Lailvaux & Irschick, 2007), higher temperatures may lead to
253 butterflies reaching adulthood faster. In line with previous studies, the overall trend of growth rate is
254 similar to a typical temperature-performance curve, with higher growth rates in intermediate to low
255 temperatures (Huey & Stevenson, 1979; Lee & Roh, 2010).

256 Growth is defined as the net energy surplus of absorption and metabolism, and thus, the
257 growth rate could be modelled by the relationship between a series of processes, including
258 metabolism and ingestion (Wood & McDonald, 1996). As temperature increases, larvae may increase
259 their ingestion rate to compensate for the increased metabolic cost (Kingsolver *et al.*, 2015). The initial
260 increase in ingestion rate may over-compensate the increase in metabolic cost if the food supply is
261 not a limiting factor, giving rise to the boosted growth rate and fitness benefits seen at 23-33°C.
262 However, this ingestion rate will eventually reach a plateau and decline beyond the optimum
263 temperature, which, in this study, is likely to be around 28°C (the mean of 23-33°C) for *H. e.*
264 *demophoon*. The reasons for the decline in ingestion could be those similar reasons involved in the
265 increased mortality rate under heat stress, eventually leading to smaller adult body mass under high
266 developmental temperatures. Whilst growth rate results match this expected metabolism-ingestion
267 relationship, we did not explicitly measure the rate of metabolism and ingestion for individual
268 caterpillars across the temperature treatments. Since the larvae in our experiments were allowed to
269 feed *ad libitum*, we do not know exactly how the rate of ingestion and metabolism are affected by
270 temperature. Future studies may look into the difference in the amount of feeding and the resulting
271 adult body mass between temperature treatments for empirical validation of the metabolism-
272 ingestion relationship.

273

274 Females respond more plastically to temperature

275 Our results found that under mildly elevated temperatures (23-33°C), females had a greater
276 increase in body mass and growth rate than males (Figures 3B and 3C). Females often have a higher
277 body mass due to a positive correlation between body size and fecundity, whereas males are typically

278 selected for larger wings, which increases their mating opportunities (Deinert *et al.*, 1994; Gotthard
279 *et al.*, 1994; Blanckenhorn *et al.*, 2007; Montejo-Kovacevich *et al.*, 2019b). This can be explained by
280 the fact that as female reproductive success is more closely correlated with adult body mass, female
281 butterflies tend to weigh more than male butterflies under fecundity selection (Blanckenhorn *et al.*,
282 2007; Gotthard, 2008). Thus, the optimal adult body mass differs between the sexes. Furthermore,
283 there were no developmental time differences between the sexes. This further supports the idea that
284 females are more plastic than males under mildly elevated temperatures, leading to increased body
285 size and growth rate (Figure 3C) (Gotthard *et al.*, 1994).

286 Wing loading, which is the mass carried per unit area of wing size, was higher in both sexes
287 under elevated temperatures (23-33°C). Greater wing loading may translate into reduced flight
288 performance and dispersal ability as shown in experiments with Monarch butterflies (Soule *et al.*,
289 2020), potentially leading to lower fitness and reproductive success despite the enhanced growth rate
290 under warmer temperatures. Similar results of the temperature-wing loading relationship are also
291 found in *Drosophila* (Frainout *et al.*, 2018). While adult body mass is correlated with higher egg
292 production and fitness, it may not benefit the butterflies in natural environments if their flight ability
293 is hindered by higher wing loading (Almbro & Kullberg, 2012). Butterflies may benefit from lower wing
294 loading to escape predators, locate host plants, or acquire mates (Molleman *et al.*, 2020). For example,
295 higher temperature reduced host-foraging motivation in parasitoid *Aphidius colemani* (Jerbi-Elayed *et*
296 *al.*, 2022) and spring generation of butterflies with more significant wing loading often disperses less
297 (Fric & Konvic, 2002; Gibbs *et al.*, 2011). Male butterflies may be under stronger selection to maintain
298 their flight ability for acquiring mates and keeping territories even when the temperature is no longer
299 a limiting factor for body mass. Thus, heavier wing loading due to greater body mass under mildly
300 elevated temperatures may be disadvantageous to male butterflies in the wild.

301

302 Conclusions

303 This study investigated the effect of temperature on the early development of butterflies and
304 the resulting adults, which has been rarely studied in tropical insects. Our findings reveal that long-
305 term sub-lethal heat stress has deleterious effects on both survival and developmental traits in a
306 common neotropical butterfly species. Eggs were found to be most vulnerable to heat stress, followed
307 by larvae. Furthermore, the growth rate followed a typical thermal-performance curve, which showed
308 an optimal growth temperature of 23-33°C. The observed decline in adult development rate and body
309 mass at 26-36°C, which is known to be correlated with lower fitness (Piyaphongkul *et al.*, 2012;
310 Klockmann *et al.*, 2017b), is of particular concern for two reasons. First, body mass may be a critical
311 restriction on *H. e. demophoon* heat stress tolerance in general (Klockmann *et al.*, 2017a, 2017b).
312 Second, because smaller females often produce fewer and/or smaller eggs, this may have a
313 transgenerational effect, resulting in offspring with lower fitness (Kingsolver & Huey, 2008; Klockmann
314 *et al.*, 2017b). The faster development rate at 23-33°C may appear to be beneficial for fecundity, but
315 it will restrict the butterfly's flight capabilities since wing size is less plastic than body mass. Ongoing
316 climate change, rising ambient temperatures, and an increase in the frequency of extreme weather
317 events such as heatwaves and drought periods would almost certainly have severe effects on life on
318 Earth (Klockmann *et al.*, 2017b; Theng *et al.*, 2020). This study emphasises the importance of
319 taking plastic responses of phenotypic traits into account when predicting population viability in
320 response to recent global warming. It calls for incorporating the effects of temperature on
321 developmental time and life-history traits into models forecasting species extinction risks (Jourdan *et*
322 *al.*, 2019).

323

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327 **Conflict of Interest**

328 The authors declare no conflicts of interest.

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332 **Contribution of authors**

333 Project design: Y.H., J.M., C.D.J., G.M.-K.; Data collection: Y.H., J.M., G.M.-K.; Data Analysis: Y.H., G.M.-
334 K.; Writing – original draft: Y.H.; Writing – review and editing: Y.H., J.M., C.D.J., G.M.-K.

335 **Data availability**

336 The data that supports the findings of this study are available in the supplementary material of this
337 article.

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