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OPEN ACCESS

1 **Parental care buffers against effects of ambient temperature on**

2 **offspring performance in an insect**

3

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9   Understanding how animals respond to and cope with variation in ambient temperature

10   is an important priority. The reason for this is that ambient temperature is a key

11   component of the physical environment that influences offspring performance in a wide

12   range of ectotherms and endotherms. Here, we investigate whether post-hatching

13   parental care provides a behavioral mechanism for buffering against the effects of

14   ambient temperature on offspring in the burying beetle *Nicrophorus vespilloides*. We

15   used a 3×2 factorial design where we manipulated ambient temperature (15, 20 or 25°C)

16   and parental care (presence or absence of a female parent after hatching). We found that

17   the effect of ambient temperature on offspring performance was conditional upon the

18   presence or absence of a caring female. Fewer larvae survived in the absence than in the

19   presence of a caring female at 15°C whilst there was no difference in larval survival at 20

20   and 25°C. Our results show that parental care buffers against some of the detrimental

21   effects of variation in ambient temperature on offspring. We suggest that post-hatching

22   parental care may buffer against such effects by creating a more benign environment or

23   by boosting offspring resilience towards stressors. Our results have important

24   implications for our understanding of the evolution of parental care because they suggest

25   that the evolution of parental care could allow species to expand their geographical range

26   to colonize areas with harsher climatic conditions than they otherwise would tolerate.

27

28   *Key words:* **ambient temperature, burying beetle, ectotherm, offspring performance,**

29   ***Nicrophorus vespilloides*, parental care.**

INTRODUCTION

Parental care is defined as any parental trait that increases the fitness of a parent's offspring, often at a cost to the parent's own fitness (Smiseth et al. 2012). Parental care evolved as a mechanism for neutralizing particular environmental hazards to offspring, such as the risks of predation and starvation (Clutton-Brock 1991; Smiseth et al. 2012). For example, it is generally accepted that the risk of predation promoted the evolution of attendance or brooding of eggs and/or juveniles, whilst the risk of starvation promoted the evolution of larger eggs, placentation and parental food provisioning after hatching or birth (Clutton-Brock 1991; Smiseth et al. 2012). There is mounting evidence that, once parental care has evolved, it can buffer against a wide range of hazards to offspring in addition to those that promoted its evolution. For example, in song sparrows (*Melospiza melodia*), post-hatching parental care buffers against the detrimental effects of high precipitation and high population density (Dybala et al. 2013). Meanwhile, in the burying beetle *Nicrophorus vespilloides*, parental care buffers against inbreeding depression in offspring (Pilakouta et al. 2015). Thus, the evolution of parental care may represent a key evolutionary innovation that provides a mechanism whereby parents can buffer against a wide range of environmental hazards that otherwise would be detrimental to their offspring.

Understanding the potential role of parental care as a mechanism for buffering against variation in ambient temperature is an important priority given that extreme weather events, including heat waves, are likely to become more frequent in the near future due to anthropogenic climate change (Stocker et al. 2013). Ambient temperature is a key component of the physical environment that influences various components of

53 offspring performance, including rate of offspring development, offspring body size and

54 offspring survival in a wide range of ectotherms (Li and Jackson 1996; Lourdais et al. 2004;

55 Wang et al. 2009) and endotherms (Dawson et al. 2005; Paul et al. 2010; de Zwaan et al.

56 2019). In birds, as well as some reptiles, parents directly buffer against variation in

57 ambient temperature by incubating their eggs (Deeming 2001, 2004). For example,

58 parent birds alter their incubation behavior in response to variation in ambient

59 temperatures (Conway and Martin 2000; Amat and Masero 2004), thereby increasing the

60 growth and survival of their offspring (Hepp et al. 2006; DuRant et al. 2003). However,

61 little is known about parental care as a mechanism for buffering against variation in

62 ambient temperature in ectotherms where parents do not incubate their eggs. As argued

63 above, once parental care has evolved, it may provide parents with a generic mechanism

64 for buffering against environmental hazards to their offspring, including suboptimal

65 ambient temperatures. Here we address this gap by comparing offspring performance at

66 different ambient temperatures in the presence or absence of parental care, using the

67 burying beetle *Nicrophorus vespilloides* as our study system.

68 The burying beetle *N. vespilloides* breeds on carcasses of small vertebrates, which

69 provide the sole source of food for the developing larvae (Scott 1998). This species is an

70 ideal study system for investigating whether parental care buffers against the effects of

71 ambient temperature on offspring performance. First, given that it is an ectotherm,

72 ambient temperature is likely to have strong effect on the performance of both offspring

73 and parents. Secondly, it has highly elaborate forms of post-hatching care that includes

74 food provisioning to offspring and defense against predators, infanticidal conspecifics and

75 microbial competitors (Eggert et al. 1997; Scott 1998). Third, post-hatching parental care

76 is facultative, which means that it is straightforward to manipulate the presence or

77   absence of parental care through parental removal experiments (Eggert et al. 1998;

78   Smiseth et al. 2003; Pilakouta et al. 2015). Forth, it is easily bred under laboratory

79   conditions, allowing for careful control of environmental conditions, including ambient

80   temperature, and monitoring of effects on the performance of offspring and their parents

81   (Eggert et al. 1998; Smiseth et al. 2003; Pilakouta et al. 2015).

82   Here we used a 3×2 factorial design where we manipulated ambient temperature

83   (15, 20 or 25°C) and parental care (presence or absence of a caring female parent after

84   hatching) and monitored subsequent effects on offspring performance (i.e., larval survival

85   and mass). 15°C represents the average summer temperature of our study population,

86   20°C the standard temperature at which laboratory populations of this species are

87   maintained (Eggert et al. 1998; Smiseth et al. 2003; Pilakouta et al. 2015), whilst 25°C

88   represents the temperature of a potential heat wave in our study area. Prior work shows

89   that offspring perform better in the presence than in the absence of caring parents

90   (Eggert et al. 1998; Smiseth et al. 2003; Pilakouta et al. 2015). Thus, if post-hatching

91   parental care buffers against the effects of variation in ambient temperature, we

92   expected an effect of the interaction between parental care and ambient temperature,

93   reflecting that the presence of a caring parent had a greater effect on offspring

94   performance (survival and/or mass) at 25°C than at 15 or 20°C. We also tested whether

95   parents pay a cost from buffering against the effects of ambient temperature on

96   offspring. If so, we expected an effect of the interaction between parental care and

97   ambient temperature, reflecting a greater difference in parental performance (weight

98   change whilst breeding and post-breeding life span) between caring and non-caring

99   females at 25°C than at 15 or 20°C.

100

METHODS

Study animals

We used virgin beetles from our outbred laboratory stock population maintained at the

University of Edinburgh. This population descended from beetles originally collected in

the wild at Corstorphine Hill (55° 56' 59" N, –3° 16' 14" E) and Hermitage of Braid (55° 55'

25" N, –3° 16' 16" E), Edinburgh, UK. All beetles were kept under 16:8 light:dark

conditions and at 20°C. Nonbreeding adults were housed individually in plastic containers

(12 × 8 × 2 cm) filled with moist soil and fed organic beef twice a week.

109

Experimental design and procedures

As mentioned above, we used a 3×2 factorial design where we manipulated both ambient

temperature (15, 20 or 25°C) and the presence or absence of a caring female parent after

hatching. 15°C matches the baseline summer temperature experienced by our study

population (the average temperatures in Edinburgh in June, July and August are 13.5,

15.3 and 15.2°C, respectively; https://en.wikipedia.org/wiki/Edinburgh). 20°C is the

baseline temperature under which laboratory populations of this species traditionally are

maintained and studied (e.g., Eggert et al. 1998; Smiseth et al. 2003; Pilakouta et al.

2015). The beetles used in our experiments had been kept under laboratory conditions

for 9–10 generations. Each generation, we recruited the same number of offspring from

each family (3 offspring) to the stock population regardless of the number of offspring

each female produced (Mattey et al. 2018). This practice limits adaptation to laboratory

122 conditions, and it is unlikely that our laboratory population were adapted to breeding at

123 20°C. Finally, 25°C represents the conditions of a potential heat wave experienced by our

124 study population (the maximum temperatures in Edinburgh for June, July and August are

125 27.8, 30.0 and 31.4°C, respectively; https://en.wikipedia.org/wiki/Edinburgh). In our

126 study species, adults tend to bury their carcasses shallowly in the leaf litter at the start of

127 breeding (Pukowski 1933). Although, this will buffer against effects of short-term

128 fluctuations in ambient temperatures, breeding beetles will still be susceptible to effects

129 of more persistent variation in ambient temperature. We therefore used a temperature

130 that was somewhat lower than the maximum temperatures to represent a heat wave.

131   We next manipulated post-hatching parental care by either removing both parents

132 on the day of hatching (absence of care) or leaving the female to care for the larvae until

133 they dispersed from the carcass (presence of care). We always removed the male on the

134 day of hatching because male assistance in post-hatching parental care is very variable in

135 *N. vespilloides* and male removal has no effect on larval performance under laboratory

136 conditions (Eggert et al. 1998; Smiseth et al. 2005). Parental removal experiments are

137 used routinely in this species and larvae survive well in the absence of care under

138 laboratory conditions (Eggert et al. 1998; Smiseth et al. 2003; Pilakouta et al. 2015).

139   At the start of the experiment, we randomly paired virgin male and female beetles

140 from our stock population. We placed each pair in a transparent plastic container (17 × 12

141 × 6 cm) filled with 1cm of moist soil. Each pair was provided with a freshly thawed mouse

142 carcass (supplied by Livefoods Direct, Sheffield, UK) with a mean (± 1SE) mass of 22.86g $\pm$

143 1.08 (range: 20–24g). At the time of pairing, we weighed all females, using this

144 information to calculate female weight change whilst breeding (see below). We then

145   placed the containers in an incubator (Qualicool 360L) pre-set to one the three ambient

146   temperatures; that is, 15, 20 or 25°C. We used a temperature probe (Elitech RC-5,

147   London, UK) to monitor ambient temperatures over time (resolution: 0.1°C; accuracy: ±

148   0.5°C). This confirmed that the mean (± SE) of the set temperatures were accurate and

149   fluctuated minimally during the experiment (15°C: mean 14.97°C ± 0.21; 20°C: mean

150   19.96°C ± 0.31; 25°C: mean 24.92°C ± 0.34). For practical reasons, we conducted our

151   experiment across 6 blocks with 2 replicate blocks for each temperature. Within each

152   block, we set up 30 breeding pairs, 15 of which were assigned to each of the two parental

153   care treatments (i.e., presence or absence of care). Thus, the total sample size of our

154   experiment was 180 breeding pairs, with 30 pairs allocated to each of the six treatments.

155   We randomized the order of the temperature treatments.

156   We recorded clutch size as the number of eggs visible through the bottom of the

157   transparent container (Monteith et al. 2012). To this end, we counted the number of eggs

158   twice a day (morning and afternoon) until eggs hatched. In the limited amount of soil we

159   used, the number of eggs visible through the bottom is positively correlated with the

160   actual number of eggs in the clutch (Pearson's correlation: $r = 0.98$, $N = 21$, $P < 0.001$;

161   Monteith et al 2012). We removed both parents on the day of hatching for broods

162   assigned to the 'absence of care' treatment, whilst we only removed the male for broods

163   assigned to the 'presence of care' treatment. We placed the removed females individually

164   in a fresh container (12 × 8 × 2 cm) filled with moist soil. We placed the females back in

165   the incubator to ensure that they were exposed to the same temperature as their

166   offspring and females that cared for their offspring. We provided removed females with

167   organic beef twice a week, as described above for the stock population.

168   We left all broods to complete their development on the carcass and monitored

169   their subsequent performance. We recorded the date and time of day (morning or

170   afternoon) at which all larvae in a brood dispersed from the carcass. We defined larval

171   dispersal as when all larvae in the brood had left the crypt surrounding the carcass, and

172   normally occurs about 4–6 days after hatching (Smiseth et al. 2003, 2005). We later used

173   this information to calculate larval development time from the date of hatching until the

174   date of dispersal. At dispersal, we counted the number of larvae in the brood and

175   weighed the whole brood. We then calculated mean offspring mass in each brood by

176   dividing brood mass by number of larvae. We transferred the brood to a fresh container

177   filled with moist soil to allow the larvae to pupate and eclose as adults. We always kept

178   these containers at 20°C to ensure that any effect on offspring until eclosion was due to

179   the ambient temperature broods were exposed to during early development on the

180   carcass. At dispersal, we weighed all females again, using this information to calculate

181   weight change whilst breeding as the difference in mass at larval dispersal and the start of

182   breeding. Prior work on this species show that caring females benefit directly in terms of

183   gaining mass by consuming from the resource (e.g., Pilakouta et al. 2016; Paquet and

184   Smiseth 2017; Grey et al. 2018). We then placed females in an individual container to

185   record their life span. At this stage, we always kept females at 20°C to ensure that any

186   effect was due to the ambient temperature females were exposed to whilst breeding. We

187   checked containers with pupae three times a week until pupae eclosed as adult beetles.

188   At the time of eclosion, we counted the number of offspring in each brood that had

189   survived until adulthood. We used this information to calculate offspring survival from

190   dispersal until eclosion.

191

192   Statistical analyses

193   All statistical analyses were conducted using the package 'car' (Fox and Weisberg 2011) in

194   R v 3.3.3 (R Core Team 2018). We analyzed data on number of eggs laid and larval survival

195   from hatching until dispersal using generalized linear models fitted with a quasi-Poisson

196   error structure to control for overdispersion. We used generalized linear models fitted

197   with a binomial error distribution to analyze data on offspring survival from dispersal to

198   eclosion. We used generalized linear models fitted with Poisson distribution to analyze

199   data on larval development time and female life span given that these response variables

200   were counts of the number of days from hatching until and the number of days until the

201   female died, respectively. Finally, we used general linear models fitted with a Gaussian

202   distribution to analyze data on mean larval mass at dispersal and female weight change.

203   We included clutch size as a predictor in all models to account for potential effects due to

204   variation in the number of eggs laid by different females. For each model, we report

205   likelihood ratios for the overall effect of temperature and the interaction between

206   temperature and parental care using the 'Anova' function in 'car'. We report estimates if

207   effect sizes with SE and z-scores or t-values for the effect of clutch size using the

208   'summary' function. For the remaining factors, we report estimates of effect sizes with SE

209   and z-scores based on Tukey tests using the package 'multcomp'. In the latter case, we

210   used Bonferroni correction to adjust p-values for multiple comparisons (Bretz et al. 2010).

211   All analyses were performed at the level of brood.

212

213   **RESULTS**

214   As predicted if post-hatching parental care buffered against the effects of ambient

215   temperature, there was a significant effect of the interaction between temperature and

216   parental care on one component of offspring performance: larval survival from hatching

217   until dispersal (Table 1; Figure 1c). However, the pattern of this interaction effect was

218   different to the one we predicted as the presence of a caring parent had a significant

219   effect on offspring performance at 15°C, but not at 20°C or 25°C (Table 1). We next

220   conducted two separate post-hoc tests to investigate in greater detail the buffering effect

221   of post-hatching parental care across our temperature range – one comparing 15 and

222   20°C and one comparing 20 and 25°C. In both cases, there was a significant effect of the

223   interaction between temperature and parental care (generalized linear models: 15 and

224   20°C: $LR\chi^2$ = 6.304, P = 0.012; 20 and 25°C: $LR\chi^2$ = 3.863, P = 0.049). Thus, the presence of

225   a caring female had a greater effect on offspring survival at 15°C than at 20°C and at 25°C

226   than at 20°C (Figure 1c). There were no effects of the interaction between parental care

227   and temperature on larval development time from hatching until dispersal, mean larval

228   mass at dispersal, or larval survival from dispersal to eclosion as an adult (Table 1; Figure

229   1a, b, d). Finally, there was no evidence that parents paid a cost from buffering against

230   the effects of ambient temperature as there was effect of the interaction between

231   parental care and temperature on either female weight change whilst breeding or female

232   life span after breeding (Table 2; Figure 2).

233   Ambient temperature had a significant main effect on the performance of both

234   offspring and their female parent (tables 1 and 2). Temperature affected clutch size

235   (generalized linear model: $LR\chi^2$ = 16.088, P = 0.0003). Females laid fewer eggs (mean ±

236   SD: 17.27 ± 11.13 eggs) at 25°C than at either 20°C (24.63 ± 10.50 eggs) (Tukey: estimate

237   0.355 ± 0.101, z = 3.522, P = 0.001) or 15°C (24.85 ± 12.73 eggs) (Tukey: estimate 0.347 ±

238 0.101, z = 3.436, P = 0.002), whilst there was no difference in number of eggs laid at 15

239 and 20°C (Tukey: estimate −0.008 ± 0.092, z = −0.089, P = 0.999). Ambient temperature

240 affected development time from hatching until dispersal (table 1), with offspring

241 developing faster at 25°C than at 20°C and 15°C, whilst there was no difference in

242 development time between 15°C and 20°C (Table 1; Figure 1a). Ambient temperature also

243 affected mean larval mass at dispersal (Table 1). Mean larval mass was higher at 20°C

244 than at either 15 or 25°C, whilst there was no difference in mean larval mass at 15 and

245 25°C (Table 1; Figure 1b). Furthermore, ambient temperature affected number of larvae

246 that survived from hatching until dispersal (Table 1). There were fewer larvae at 25°C

247 than at either 15 or 20°C, whilst there was no difference in number of larvae at 15 and

248 20°C (Table 1; Figure 1c). Ambient temperature affected female weight change from the

249 onset of breeding until larval dispersal (Table 2). Females gained more weight whilst

250 breeding at 15°C than at either 20 or 25°C, but there was no difference in female weight

251 change whilst breeding at 20 and 25°C (Table 1; Figure 2a). Ambient temperature had no

252 effects on offspring survival from dispersal until eclosion as an adult (Table 1; Figure 1d)

253 or female life span after breeding (Table 2; Figure 2b).

254   Post-hatching parental care had a positive main effect on mean larval mass,

255 number of larvae at dispersal, and offspring survival from dispersal until eclosion (Table 1;

256 Figure 1b–d). There was also a difference in weight change whilst breeding between

257 caring and non-caring females (Table 2). Caring females tended to gain weight whilst

258 breeding whilst non-caring females tended to lose weight (Figure 2a). Post-hatching

259 parental care had no effect on offspring development time (Table 1; Figure 1a) and there

260 was no difference in life span after breeding between caring females and females that

261 had been removed (Table 2; Figure 2b).

262

DISCUSSION

264   We found that the presence of a caring female had a significant effect on offspring

265   performance at 15°C but not at 20 or 25°C. This finding has important implications by

266   showing that the benefits of post-hatching parental care to offspring are temperature

267   dependent. One potential explanation for why the benefits of parental care may be

268   temperature dependent in ectotherms is that their performance tend to increase with

269   rising temperatures until reaching an optimum after which performance declines rapidly

270   until reaching the critical thermal maximum (Huey and Stevenson 1979; Stillman 2003;

271   Deutsch et al. 2008). Unfortunately, there are no thermal performance curves for our

272   study species. Nevertheless, based on the explanation suggested above, we anticipated

273   offspring performance to peak at 25°C given that this temperature is near or below the

274   critical thermal maximum for most insects (24–40°C; Deutsch et al. 2008; Martin and

275   Huey 2008; Estay et al. 2013). Thus, our finding that offspring performance peaked at 15

276   or 20°C provides no support for this explanation. An alternative explanation for our

277   finding is that, whilst breeding on carcasses of small vertebrates, larvae compete with

278   microbes for access to resources (Rozen et al. 2008). Given that ambient temperature

279   also determines decay of carrion due to microbial growth (Xu et al. 2016), the finding that

280   larval survival was lowest at 25°C suggests that ambient temperature may have had a

281   differential effect on the competitive ability of larvae and microbes. Furthermore, given

282   that caring parents are known to suppress microbial growth in this species (Rozen et al.

283   2008), the effect of the interaction between ambient temperature and parental care

284   suggests that the presence of a caring female had a differential effect on the outcome of

285   competition between larvae and microbes depending on the ambient temperature.

286   Further work is now needed to investigate this suggestion.

287   We found that larval survival from hatching until dispersal was highest at 15°C in

288   the presence of a caring parent. Given that 15°C closely matches the average daily

289   summer temperatures in the study area and parents normally provide care for their

290   broods, this suggests that larvae of our population are well adapted to the conditions

291   normally encountered in the wild. We also found that the larvae had substantially lower

292   survival in the absence than in presence of a caring female at 15°C. This finding has

293   important implications by suggesting that the evolution of elaborate post-hatching

294   parental care has allowed this species to extend its geographical range to areas with a

295   colder climate than it otherwise would tolerate. A recent study on another species within

296   the genus *Nicrophorus*, *N. sayi*, suggests the evolution of post-hatching parental care has

297   allowed this species to shift its seasonal activity by breeding under cold conditions in early

298   spring, potentially as a means to avoid competition for resources with its congeners

299   (Benowitz et al. 2019). Thus, although post-hatching parental care in this genus is thought

300   to have evolved in response to inter- and intraspecific competition over carrion (Eggert

301   and Müller 1997; Scott 1998), the generic buffering capacity of parental care may have

302   allowed these species to expand their geographical range and/or seasonal activity. This

303   suggestion has important implications for our understanding of the evolution of post-

304   hatching parental care by providing a potential explanation for why it tends to be obligate

305   in most species. The reason for this is that any expansion of geographical range or

306   seasonal activity to environmental conditions that otherwise cannot be tolerated would

307   effectively prevent any secondary losses of post-hatching parental care.

308   Our study raises questions about the potential mechanisms for how caring parents

309   may buffer against the effects of variation in ambient temperature on offspring

310   performance. In birds and some reptiles, parents can directly buffer against variation in

311   ambient temperature by incubating their eggs (Deeming 2001, 2004), but this mechanism

312   is not available for our study species given that parents do not incubate their eggs. We

313   propose three mechanisms for how parental care might provide a generic mechanism for

314   buffering against suboptimal ambient temperatures: (1) parents facultatively adjust the

315   amount of care they provide in response to variation in ambient temperature, thereby

316   compensating for any detrimental effects at suboptimal temperatures, (2) caring parents

317   create a more benign environment that minimizes effects of other hazards to the

318   offspring, such as the risks of starvation or infection, thereby buffering against any

319   detrimental effects at suboptimal temperatures, and (3) parents enhance their offspring's

320   growth and condition, thereby facilitating the offspring's own ability to cope with the

321   otherwise detrimental effects at suboptimal temperatures. If females provided more care

322   at 15°C as compared to 20 and 25°C, we expected the former females to pay some cost in

323   terms of loosing more mass (or gaining less) or a shorter life span. In contrast, we found

324   no effect of the interaction between ambient temperature and parental care influenced

325   female performance (i.e., female weight change whilst breeding or life span after

326   breeding). Thus, we found no evidence in support for the first explanation, suggesting

327   that the buffering effect of post-hatching parental care is independent of any plastic

328   responses by parents to changing temperature. Our results cannot differentiate between

329   the second and third explanation. Nevertheless, we found that post-hatching parental

330   care had a positive impact on mean larval mass, lending some tentative support for the

331   third mechanism. There is now need for further work to investigate the mechanistic basis

332   for how caring parents buffer against the effects of thermal stress on their offspring.

333   Finally, our results have implications for our understanding of the potential role of

334   parental care as a behavioral mechanism for mitigating the detrimental effects of rising

335   temperatures due to anthropogenic climate change. Prior work has focused on how

336   individuals alter their own behavior in response to rising temperatures, thereby

337   mitigating some of the detrimental effects of climate change to themselves (Kearney et

338   al. 2009; Beever et al. 2017). Here we show that post-hatching parental care – a social

339   behavior that is expressed in parents but that affects the offspring's fitness – can mitigate

340   some of the effects of ambient temperature on offspring performance. There is now a

341   need for further studies that extend our work to other taxa with parental care or similar

342   social behaviors that might buffer against climate change and that expand our

343   manipulations to a wider range of temperatures. Furthermore, there is a need for

344   comparative work examining whether social species are better at coping with thermal

345   stress associated with climate change than solitary ones.

346   In conclusion, we show that post-hatching parental care buffered against the

347   effects of ambient temperature on offspring performance, and that this buffering effect

348   may be independent of any plastic responses by parents to changing temperature.

349   Instead, post-hatching parental care may buffer against the effects of ambient

350   temperature by creating a more benign environment for the offspring or by boosting the

351   offspring's condition and thereby their resilience towards stressors. Our results highlight

352   the need to understand how parental care and other social behaviors may determine how

353 well animal populations respond to and cope with extreme weather conditions, the

354 frequency of which is expected to increase due to anthropogenic climate change.

355

362 Data accessibility: Analyses reported in this article can be reproduced using the data

363 provided by Grew et al. (2019)

364

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466   **Table 1**

467   **General linear and generalized linear models testing for effects of ambient temperature (15, 20 or 25°C), post-hatching parental care**

468   **(presence or absence of caring parents) and the interaction between them on four measures of offspring performance: development time**

469   **from hatching to dispersal, mean mass at dispersal, number of offspring at dispersal, and survival from dispersal to eclosion. All test**

470   **statistics are z-scores, expect for the overall effect of temperature and the interaction between temperature and parental care, which are**

471   **likelihood ratios ($LR\chi^2$) (indicated by *) and for the effect of clutch size on mean mass at dispersal and number of offspring at dispersal,**

472   **which are t-values (indicated by †). See main text for further details on the statistical analyses.**

Development time from hatching to dispersal	Estimate	SE	Test statistic	P-value
Temperature			20.574*	<0.0001
15°C vs. 20°C	0.061	0.087	0.695	0.764
15°C vs. 25°C	0.371	0.116	3.203	0.004
20°C vs. 25°C	0.310	0.116	2.639	0.022
Parental care (present vs. absent)	−0.048	0.083	−0.577	0.564
Clutch size	0.0005	0.003	0.193	0.847
Temperature*Parental care			0.346*	0.841
15°C present vs. 15°C absent	−0.031	0.081	−0.381	0.999

20°C present vs. 20°C absent	−0.048	0.083	−0.577	0.992
25°C present vs. 25°C absent	0.041	0.128	0.321	>0.999
Mean mass at dispersal				
Temperature			15.808*	0.0004
15 vs. 20°C	−0.027	0.020	−2.657	0.021
15 vs. 25°C	0.012	0.012	1.036	0.552
20 vs. 25°C	0.039	0.012	3.252	0.003
Parental care (present vs. absent)	0.054	0.009	4.860	<0.0001
Clutch size	0.042	0,006	7.563†	<0.0001
Temperature*Parental care			2.911*	0.233
15°C present vs. 15°C absent	0.068	0.009	7.215	<0.0001
20°C present vs. 20°C absent	0.046	0.009	4.860	<0.0001
25°C present vs. 25°C absent	0.060	0.013	4.799	<0.0001
Number of offspring at dispersal				
Temperature			37.481*	<0.0001
15°C vs. 20°C	−0.417	0.206	−2.020	0.102
15°C vs. 25°C	1.193	0.374	3.192	0.0038
20°C vs. 25°C	1.610	0.360	4.475	<0.001

Parental care (present vs. absent)	−0.058	0.181	−0.318	0.751
Clutch size	0.042	0.006	7.563†	<0.0001
Temperature*Parental care			7.622*	0.022
15°C present vs. 15°C absent	0.578	0.196	2.946	0.034
20°C present vs. 20°C absent	−0.058	0.181	−0.318	>0.999
25°C present vs. 25°C absent	0.801	0.399	2.007	0.320
Survival from dispersal to eclosion				
Temperature			5.289*	0.071
15°C vs. 20°C	0.996	0.702	1.420	0.327
15°C vs. 25°C	−0.496	0.925	−0.537	0.852
20°C vs. 25°C	−1.492	0.919	−1.625	0.232
Parental care (present vs. absent)	1.792	0.724	2.474	0.013
Clutch size	0.022	0.028	0.811	0.418
Temperature*Parental care			0.602*	0.740
15°C present vs. 15°C absent	2.389	1.222	1.955	0.353
20°C present vs. 20°C absent	1.792	0.724	2.474	0.123
25°C present vs. 25°C absent	−0.299	0.939	0.319	0.958

474 **Table 2**

475 **General linear and generalized linear models testing for effects of ambient temperature (15, 20 or 25°C), post-hatching parental care**

476 **(presence or absence of caring parents) and the interaction between them on two measures of the performance of the female parent:**

477 **weight change from start of breeding until larval dispersal, and life span. All test statistics are z-scores, expect for the overall effect of**

478 **temperature and the interaction between temperature and parental care, which are likelihood ratios ($LR\chi^2$) (indicated by *) and for the**

479 **effect of clutch size on weight change, which is a t-value (indicated by †). See main text for further details on the statistical analyses.**

Weight change	Estimate	SE	Test statistic	P-value
Temperature			28.223*	<0.0001
15°C vs. 20°C	0.028	0.009	2.904	0.010
15°C vs. 25°C	0.052	0.011	4.939	<0.001
20°C vs. 25°C	0.024	0.011	2.203	0.070
Parental care (present vs. absent)	0.034	0.010	3.599	0.0003
Clutch size	−0.0005	0.0003	−1.757†	0.081
Temperature*Parental care			3.540*	0.170
15°C present vs. 15°C absent	0.021	0.009	2.273	0.204
20°C present vs. 20°C absent	0.034	0.010	3.599	0.004

25°C present vs. 25°C absent	0.048	0.011	4.427	<0.0001
Life span				
Temperature			3.782*	0.151
15°C vs. 20°C	−0.003	0.033	−0.076	0.997
15°C vs. 25°C	0.063	0.037	1.732	0.193
20°C vs. 25°C	0.066	0.038	1.747	0.187
Parental care (absent vs. present)	−0.020	0.032	−0.613	0.540
Clutch size	0.002	0.0009	2.294	0.022
Temperature*Parental care			3.502*	0.174
15°C present vs. 15°C absent	0.041	0.032	1.284	0793
20°C present vs. 20°C absent	−0.020	0.033	−0.613	0.990
25°C present vs. 25°C absent	0.069	0.038	1.834	0.442

480

481 **Figure legends**

482

483 **Figure 1**

484 Effects of ambient temperature (15, 20 or 25°C), post-hatching parental care (presence or

485 absence of caring parents) and the interaction between them on four measures of

486 offspring performance: development time from hatching to dispersal (a), mean mass at

487 dispersal (b), number of offspring at dispersal (c), and survival from dispersal to eclosion

488 (d). Drawn from raw data and representing means ± 1 SE. The sample sizes for

489 development time from hatching to dispersal, mean mass at dispersal and survival from

490 dispersal to eclosion were: 15°C and female present (N = 27), 15°C and female absent (N =

491 19), 20°C and female present (N = 27), 20°C and female absent (N = 20), 25°C and female

492 present (N = 15), and 25°C and female absent (N = 11). The sample sizes for number of

493 offspring at dispersal were: 15°C and female present (N = 29), 15°C and female absent (N

494 = 28), 20°C and female present (N = 30), 20°C and female absent (N = 30), 25°C and

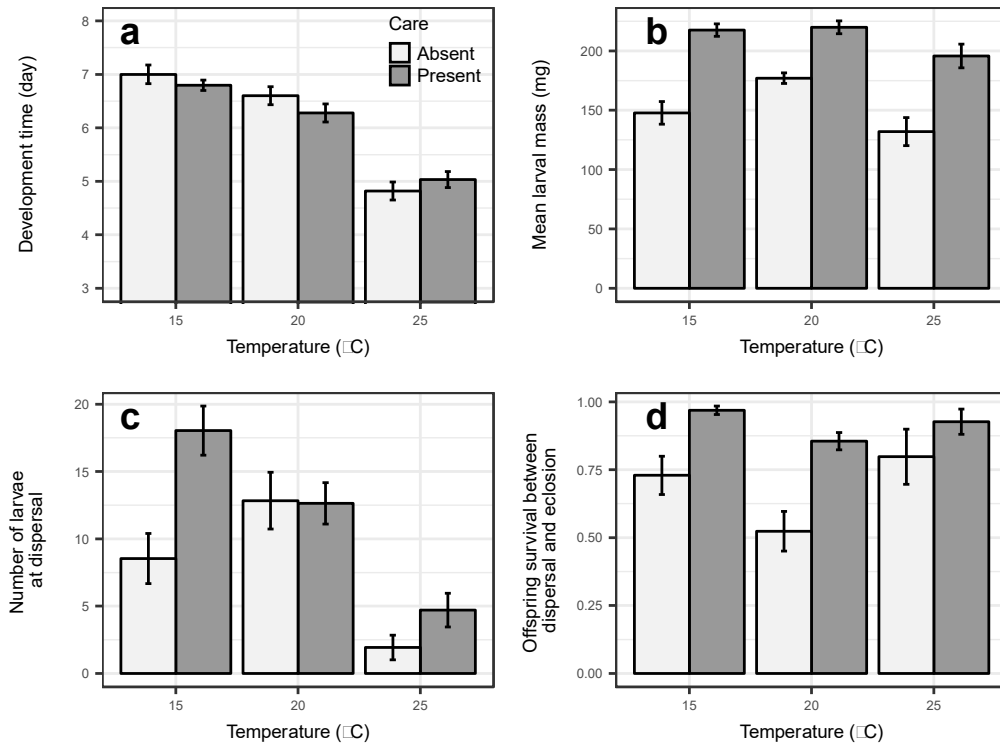495 female present (N = 28), and 25°C and female absent (N = 29).

496

497   **Figure 2**

498   Effects of ambient temperature (15, 20 or 25°C), post-hatching parental care (presence or

499   absence of caring parents) and the interaction between them on female weight change

500   whilst breeding (a) and female life span after breeding (b). Drawn from raw data and

501   representing means ± 1 SE. The sample sizes for weight change were: 15°C and female

502   present (N = 27), 15°C and female absent (N = 26), 20°C and female present (N = 28), 20°C

503   and female absent (N = 23), 25°C and female present (N = 22), and 25°C and female

504   absent (N = 17). The sample sizes for life span were: 15°C and female present (N = 26),

505   15°C and female absent (N = 25), 20°C and female present (N = 27), 20°C and female

506   absent (N = 22), 25°C and female present (N = 21), and 25°C and female absent (N = 17).
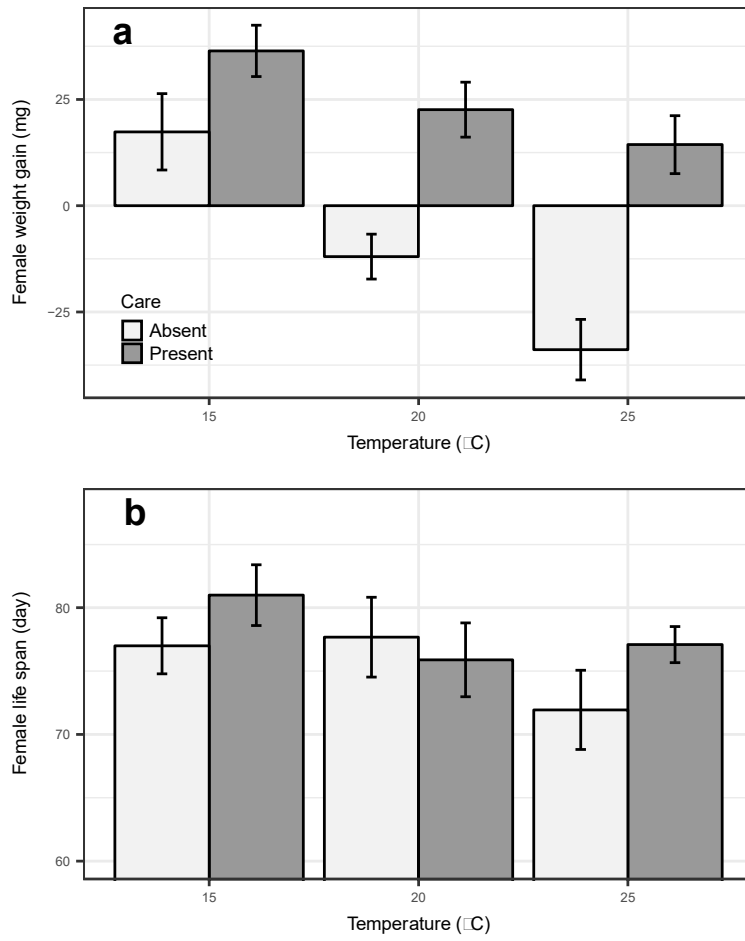
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509   Figure 1

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512   Figure 2

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