Effects of early and late life environments on ageing

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Abstract

Early and late life environments can interact in complex ways to influence the fitness of individuals. Most studies investigating effects of the environment on fitness focus on environments experienced and traits expressed at a single point in an organism's life. However, environments vary with time, thus the environments organisms experience at different ages may interact to affect how traits change throughout life. Here, we test whether thermal stress experienced during development leads individuals to cope better with thermal stress as adults. We manipulated temperature during both development and adulthood and measured a range of life-history traits, including senescence, in male and female seed beetles, *Callosobruchus maculatus*. We found that favourable developmental conditions increased reproductive performance of females (i.e. silver-spoon effects). In contrast, non-reproductive traits such as lifespan and survival senescence were only affected by adult environments- high adult temperatures decreased longevity and survival. Additionally, developmental and adult environments interacted to affect age-dependent changes in male weight. Overall, our results show that effects of early and late environments can be both sex- and trait- specific, and that a full understanding of how environments interact to affect fitness and ageing requires the integrated study of conditions experienced during different stages of ontogeny.

Keywords: silver-spoon effect, matching environments, phenotypic plasticity, beneficial acclimation, *Callosobruchus maculatus*, senescence.

24 **Introduction**

25 Early life conditions can act directly on developing phenotypes and in consequence
 26 can have both immediate and long-lasting effects on a range of fitness-related traits
 27 (Frankenhuis et al, 2019, van de Pol, Bruinzeel et al, 2006). For example, various studies (e.g.
 28 Descamps et al, 2008; Klepsatel et al, 2019, 2020; Madsen & Shine, 2000; Muller et al, 2016;
 29 Sanghvi et al, 2021; Wong & Kolliker, 2014) have shown that developmental environments
 30 can create “silver-spoon effects” (Grafen, 1988; Monaghan, 2008), where individuals who
 31 experience a favourable early environment have increased fitness and performance as adults,
 32 compared to individuals who experience poor developmental conditions.

33 The effects of early life environments on fitness are also expected to depend on
 34 conditions experienced later in life (Gluckman et al, 2005, Monaghan, 2008). It has been
 35 suggested that individuals experiencing certain conditions during development may adjust
 36 their phenotype to improve performance when exposed to the same conditions as adults
 37 (“environmental matching” or predictive adaptive response). Under this scenario, early life
 38 conditions shape the phenotype in response to predicted adult conditions, so that fitness is
 39 optimised when environments experienced during development and adulthood match
 40 (Bateson et al, 2014; Beaman et al, 2016; Cleal et al, 2007; Hayward & Lummaa, 2013). A
 41 special case of the environmental matching hypothesis, the “beneficial acclimation” response,
 42 (Huey et al, 1999; Woods & Harrison, 2002), deals explicitly with stressful developmental
 43 and adult temperatures. It predicts that stressful temperatures experienced during development
 44 acclimate individuals so they perform better when they also experience these stressful
 45 temperatures as adults, compared to individuals who only experience stress as adults and not
 46 during development (e.g. Bahnrdoff et al, 2016; Deere & Chown, 2006; Kellermann et al,
 47 2017; Kristensen, 2008; Scharf et al, 2015; Scott & Johnston, 2012). Another hypothesis

48 which predicts that adult environments are important for determining later life fitness
 49 consequences of early life environments is the “environmental saturation” hypothesis
 50 (Engqvist & Reinhold 2016; Pigeon et al, 2019). This hypothesis predicts that in favourable
 51 adult environments, all individuals will perform well regardless of their developmental
 52 environment, and likewise, that all individuals will perform poorly in bad adult environments.
 53 Thus, effects of developmental environments on adult phenotypes are only evident in
 54 intermediate adult environments (e.g. Pigeon et al, 2019).

55 Empirical evidence from studies looking at how early and late life environments
 56 interact to affect adult traits is not clear cut, and indicates that the various hypotheses
 57 employed to explain the relationships between phenotypic and environmental variation are not
 58 mutually exclusive (Pigeon et al, 2019). For instance, some studies find evidence for
 59 beneficial environmental matching (Duxbury & Chapman, 2020), while others find other
 60 types of interactive (Briga et al, 2017), or only additive (Kleinteich et al, 2015) effects of
 61 exposure to poor conditions during both early and late life. Additional complexity to the
 62 tangled interactions between early and late life conditions arises from the fact that responses
 63 to environmental stimuli can be trait- and sex-dependent (e.g. Duxbury & Chapman, 2020;
 64 Helle et al, 2012; Krause et al, 2017; Min et al, 2020; Pigeon et al, 2019; Santos et al, 2021;
 65 Scharf, Braf et al, 2015; Stillwell & Fox, 2005). For example, in cichlids reproductive rate is
 66 determined only by nutrition during development, while adult growth rate is determined only
 67 by nutrition in the adult stage, and clutch size is determined by both developmental and adult
 68 life nutrition (Taborsky, 2006). Differences in the way the environment affects different traits
 69 may result from energetic and physiological constraints acting on life-history traits (Partridge
 70 and Silby 1991), as well as the necessity to allocate resources across traits. Furthermore,
 71 differences between males and females in their life-histories and mating strategies mean that
 72 selection might favour males and females to respond differently to the same environment
 73 (Ceballos & Valenzuela 2011; Maklakov et al, 2009; Stillwell et al. 2010). For example, in

74 seed beetles, males and females respond differently to the presence and density of competitors
75 during the larval stage, leading to sex-specific differences in a variety of life-history traits
76 (Iglesias-Carrasco et al 2020; Sanghvi et al, 2021).

77 Research shows that, in addition to influencing the absolute expression of traits, the
78 environment can also influence how traits change over an individual's life, and specifically
79 how they deteriorate with advancing age (i.e. how they senesce) (Balbontin & Moller, 2015;
80 Nussey et al, 2007). Senescence occurs as a consequence of relaxed selection on fitness-
81 related traits in older individuals due to trade-offs between life-history components (Rose &
82 Charlesworth, 2002; Stearns, 1989). However, the rate at which individuals age may depend
83 on a range of factors such as their sex and external environment (e.g. Sanghvi et al, 2021).

84 While there is some support for silver-spoon effects on ageing, with favourable
85 developmental conditions leading to slower reproductive and survival senescence (Hayward,
86 Wilson et al, 2013, Cooper and Kruuk, 2018, Sanghvi et al, 2021), an alternative hypothesis
87 suggest that individuals experiencing good environments may senesce faster due to increased
88 investment in growth and reproduction when young (Adler et al, 2016; Hooper et al 2017;
89 Hunt et al, 2004; Spagopoulou et al, 2020). Additionally, senescence can also depend on the
90 interactions between developmental and adult environments, as seen in studies which test for
91 compensatory growth. Here, organisms which experience poor developmental environments
92 increase their investment in growth in favourable adult environments, although at the cost of
93 increased mortality (Dmitriew & Rowe, 2007; Metcalfe & Monaghan, 2001). While recent
94 research has begun investigating how interactions between developmental and adult
95 environments affect survival and reproductive senescence (Duxbury & Chapman, 2020; Min
96 et al, 2021; Zajitschek et al, 2009), the results do not clearly support one hypothesis (silver-
97 spoon, matching environment, or environmental saturation). Additionally, the age-dependent
98 changes in traits measured are restricted to survival and reproduction, and do not consider
99 other traits which can also change with age and influence fitness.

Here we test whether interactions between heat stress experienced during development and adulthood, if present, are beneficial or not, on various life-history traits, including senescence, in male and female seed beetles (*Callosobruchus maculatus*). Temperature is known to be crucial in determining life-history traits, including senescence, and physiology of ectotherms (Zuo et al, 2012) and is often manipulated in studies which test for silver-spoon effects (e.g. Scharf, Braf et al, 2015), matching environments (e.g. Min et al, 2021), and beneficial acclimation (e.g. Leroi et al, 1994), making it ideal for our experiment. In seed beetles, hot temperatures have been shown to be stressful to survival and reproduction (Fox et al, 2011; Stillwell & Fox, 2005; Stillwell et al, 2007; Vasudeva et al, 2014). However, it is unknown how unfavourable temperatures at different life stages interact with each other to affect senescence, and whether these interactions can be beneficial.

111

112 **Methods**

113 *Origin and maintenance of study species*

Our stock population of *C. maculatus* was sourced in 2017 from stock kept at the University of Western Australia (see Dougherty et al, 2017 for maintenance details). Once in our lab, stock was maintained for 14-16 generations on cowpea beans (*Vigna unguiculata*) at 24°C - 28°C and 20% - 40% relative humidity. Neither stock nor experimental beetles were provided food or water as adults because they do not need to feed or drink as adults in order to survive and reproduce (Beck & Blumer, 2014).

120

121 *Experimental design*

To test the effects of developmental and adult temperatures on life-history traits and senescence, we used a split-brood full-sib 2x2 factorial design, in which beetles were assigned to either ‘ancestral’ temperatures (23°C - 25 °C) or ‘hot’ temperatures (33°C - 36°C) during

125 development, and then ancestral or hot temperatures as adults. The ancestral temperature was
126 at the lower end of the temperature range in which the stock had been raised for over 14-16
127 generations. The hot temperature was a novel and unfavourable environment for this
128 population.

129 To breed experimental beetles, we collected 86 male and 86 female virgin seed beetles
130 from 150 isolated stock beans, within an hour from when they emerged. Virgin females were
131 randomly paired with virgin males for mating and then given 20-30 beans on which to lay
132 eggs (at 24°C). The beans were checked for eggs every two hours, and those with a single egg
133 laid on them were transferred to individual Eppendorf tubes. If a bean had more than one egg
134 laid on it, the extra eggs were scraped off. Eppendorf tubes containing a bean with an egg,
135 were then randomly assigned to a hot (33°C - 36°C) or ancestral (23°C - 25 °C) developmental
136 temperature for incubation until adults emerged.

137 On the day of emergence, beetles were weighed (to the nearest 0.01 mg) using a
138 Sartorius Cubis microbalance, and their developmental time (in days) and sex were recorded.
139 Beetles were then assigned to either the hot or ancestral adult temperature treatment, in which
140 they remained until they died. This generated four treatments: *ancestral developmental and*
141 *ancestral adult (AA)*, *ancestral developmental and hot adult (AH)*, *hot developmental and*
142 *ancestral adult (HA)*, and *hot developmental and hot adult (HH)* temperatures (See Table S1
143 in Supplement for sample sizes). Males were kept in Eppendorf tubes and weighed every
144 second day. Females were individually mated with a single male from our stock population on
145 the day of their emergence, then transferred to a Petri dish and given 15 new beans each day
146 to lay eggs on. To ensure that all females mated, we observed whether or not the female
147 kicked the male with her hind legs to end copulation (if she did not, we paired her with the
148 same male again after ~20 minutes). Beans with eggs laid on them were stored in plastic bags,
149 and frozen at -20°C for counting later. Both sexes were checked daily for survival and their
150 adult lifespan was recorded. Details of all traits measured are given in Table 1.

151 The experiment was conducted over three experimental blocks (Block 1: 26 families;
152 Blocks 2 and 3: 30 families each). The individuals used in the three experimental blocks came
153 from 3 successive generations of stock beetles (i.e. blocks 1, 2, and 3, correspond to
154 generations 14, 15, and 16 respectively). Some experimental beetles escaped, were killed
155 accidentally, or could not have their sex identified accurately during the experiment, and were
156 therefore excluded from analyses of reproduction, weight, and lifespan (57 excluded out of
157 1381 beetles). The assignment of beetles to the developmental and adult treatments was
158 random except that we tried to assign beetles of each sex from each of the 86 families equally
159 across the four treatments. The observer was blinded to the treatment of beetles during data
160 collection to avoid bias.

161

162 *Data analysis*

163 To determine the effects of developmental and adult temperature as well as their
164 interaction on the life-history traits (age-independent traits) and senescence (age-dependent
165 traits) of male and female seed beetles, we used Generalised Linear Mixed-effects Models
166 (GLMM) or Linear Mixed-effects Models (LMM) as appropriate. All analyses were
167 conducted in R v3.5.2 (R Development Core Team, 2011) and models were built using the
168 *lme4* (Bates et al, 2014), and *glmmTMB* (Magnusson et al, 2017) packages. Model details for
169 each analysed trait are given in Table 1, and in Section B of the online supplement. All
170 models contained experimental block as a three-level fixed effect, and beetle family (i.e. full-
171 sibling groups) as a random effect unless mentioned otherwise. For traits measured prior to
172 the assignment of adult treatments (i.e. emergence success, development time, and emergence
173 weight), we included developmental temperature in the model as a fixed effect. For traits
174 measured after beetles were assigned to adult temperatures (i.e. adult lifespan, female fertility,
175 female lifetime reproductive success, age-dependent (daily) female fecundity, age-dependent
176 male weight, and age-dependent survival), we included both developmental and adult

temperatures as well as their interactions as fixed effects. For age-dependent female fecundity and age-dependent male-weight, we included adult lifespan as a fixed effect in the models to account for selective disappearance of beetles. Additionally, for male and female lifespan we included emergence weight as a covariate because larger seed beetles have been previously shown to live longer (Fox et al, 2003). For age-dependent weight of males, emergence weight was also included as a covariate, although here, as an interaction with age, because males at different ages could be affected by their emergence weight in different ways.

We conducted two post-hoc tests to examine how developmental temperatures were affecting age-dependent male weight, within each adult temperature. The first post-hoc model only used data from males who experienced hot adult temperatures, to compare males in AH (ancestral developmental and hot adult) vs HH (hot developmental and hot adult) treatments. The second only used data from males who experienced ancestral adult temperatures, so that males in HA (hot developmental and ancestral adult) and AA (ancestral developmental and ancestral adult) temperatures could be compared.

For female age-dependent (daily) fecundity, we additionally created three models, one which allowed the slopes of different families (of full-sibs) to differ, the other which allowed the slopes of different females to differ, and the third which allowed slopes of both different females and different families to differ. These models were then compared using Akaike information Criteria and log-likelihood ratio tests with the *anova* function in the *stats* package to obtain the best fitting model. This was done to test whether different families and females showed different pattern of reproductive senescence from each other.

For all adult traits, males and females were analysed separately because we were not interested in comparing effects across the sexes (i.e. interactions with sex). For age-independent traits, where models contained interactions, we ran a “full” model with the interactions, as well as a “main-effects” model (if the interactions in the full model were non-significant). The main-effects models excluded non-significant interactions to allow accurate

203 interpretation of the main-effects (Engqvist, 2005). For all linear models, residuals were
 204 checked visually to ensure they met assumptions of normality and homoscedasticity. When
 205 they did not, the response variable was transformed. To test for overdispersion in our models,
 206 we used the function *simulateResiduals* in the package *DHARMa* (Hartig 2020). Where there
 207 was evidence for over-dispersion (i.e. for female lifetime reproductive success), we fitted an
 208 observation level random effect (Harrison, 2014). To test whether the effects of
 209 developmental temperatures were consistent across all blocks, analyses for age-independent
 210 traits were followed by post-hoc pairwise comparisons of hot and ancestral developmental
 211 temperatures within each block. These comparisons were done using Tukey’s test in the
 212 *emmeans* package (Lenth et al, 2019). Effect sizes were calculated as “Hedge’s g” for all two-
 213 group comparisons (following equations (1) and (2) in Nakagawa & Cuthill, 2007).

214

215 **Results**

216 Our analyses indicated a range of effects of developmental and adult temperature on male and
 217 female traits. We describe these results below, and provide a summary in Table 2, with
 218 complete model outputs for all analyses presented in the supplementary material (Tables S3 –
 219 S18).

220

221 *Age-independent traits*

222 Hot temperatures caused lower emergence success, faster development, and lower
 223 emergence weight in beetles, than ancestral temperatures. Specifically, hot developmental
 224 temperature reduced the *emergence success* of beetles ($P < 0.001$, Table S3): 676 out of 864
 225 eggs (78%) emerged as adult beetles from the ancestral developmental temperature, while 705
 226 out of 1439 eggs (49%) emerged as adult beetles from the hot developmental temperature.
 227 Both males and females that experienced hot developmental temperatures had a shorter

228 *development time* (mean $\pm$ SE: males= 23.1 $\pm$ 0.1, females= 23.5 $\pm$ 0.2 days) than those
 229 experiencing ancestral developmental temperatures (mean $\pm$ SE: males= 37.8 $\pm$ 0.2, females=
 230 37.99 $\pm$ 0.2 days) ($P < 0.001$ for both males and females, Hedge's g : males= 4.41, females=
 231 4.962, Table S4). Further, both males and females which developed in the hot temperature
 232 had a lower *emergence weight* (mean $\pm$ SE: males= 3.510 $\pm$ 0.030, females= 4.710 $\pm$ 0.039
 233 mg) than those developing in the ancestral temperature (mean $\pm$ SE: males= 3.750 $\pm$ 0.030,
 234 females= 5.760 $\pm$ 0.042 mg) ($P < 0.001$ for both sexes, Hedge's g : males= 0.436, females=
 235 1.4, Table S5).

236 After controlling for the positive effect of emergence weight ($P < 0.001$, Section E in
 237 supplement) there were contrasting effects of hot temperatures in the developmental versus
 238 adult stage on *adult lifespan*. For both males and females, hot developmental temperatures
 239 increased adult lifespan (Males: Hedge's g = 0.10; P = 0.005, Females: Hedge's g = 0.06; P =
 240 0.036). In contrast, hot adult temperatures decreased male and female adult lifespan (Males:
 241 Hedge's g = 4.820; $P < 0.001$, Females: Hedge's g = 2.493; $P < 0.001$) (Figure 1, Tables S6 and
 242 S7). There was no significant interaction between developmental temperature and adult
 243 temperature on adult lifespan on either males (P = 0.251), or females (P = 0.531).

244 Females that developed in hot temperatures were less likely to be *fertile* than females
 245 which developed in ancestral temperatures (15.5% of females from the hot developmental
 246 temperature did not lay any eggs compared to 0.6% of females from the ancestral
 247 developmental temperature, $P < 0.001$, Table S8). Neither adult temperature on its own (P =
 248 0.119), nor the interaction between developmental and adult temperatures (P = 0.986), had a
 249 significant effect on female fertility. In contrast, both hot developmental ($P < 0.001$) and hot
 250 adult ($P < 0.001$) temperatures reduced the *Lifetime Reproductive Success (LRS)* of females,
 251 compared to ancestral temperatures (Figure 2, Table S9). Although, developmental
 252 temperatures (Hedge's g = 0.945) had a greater effect than adult temperature (Hedge's g =

0.241) on the LRS of females. There was no effect of the interaction between developmental and adult temperatures on female LRS ($P = 0.595$).

The effects of developmental environments seen in the results above were consistently found within each block, except for male and female adult lifespan (Table S10).

Age-dependent traits

Females that experienced either hot developmental or hot adult temperatures showed a steeper decline in *age-dependent (daily) fecundity* as they aged compared to females that experienced ancestral temperatures at either stage (for both stages $P < 0.001$; Table S11). Females from hot adult temperatures laid a higher number of eggs than females from ancestral adult temperatures at ages one (Hedge's $g = 0.82$), two (Hedge's $g = 0.50$), and three (Hedge's $g = 0.134$) days. After day 3, the effect sizes showed the opposite pattern i.e. females from ancestral adult temperature laid more eggs (Table S12). There was no three-way interaction between developmental temperature, adult temperature, and age (as either linear ($P = 0.525$) or quadratic ($P = 0.226$)) to affect the age-dependent (daily) fecundity (Figure 3; Table S11).

The model which allowed the slopes for age-dependent (daily) fecundity to vary between families and between females, provided a better fit to the data than models which allowed only the slopes of different families (of full-sibs) to vary, or only the slopes of different individuals to vary, or only the intercepts of families and individuals to vary (Table S13). This suggests both significant between-family and between-individual variation in female reproductive senescence rates.

There was a significant effect of the three-way interaction between developmental and adult temperatures, and age, on age-dependent *male weight* ($P < 0.001$, Table S14, Figure 4). Post-hoc models, which analysed age-dependent weight data for hot adult and ancestral adult treatments separately (Tables S15, S16), each revealed an interaction between developmental temperature and age. Specifically, in both hot (Table S15) and ancestral (Table S16) adult

279 environments, males who experienced hot temperature during development had a lower rate
280 of decline in weight with age compared to males who experienced ancestral temperatures
281 during development. The difference in average rate of decline in weight per day was greater
282 between HH and AH treatments (0.049 mg per day) than between AA and HA treatments
283 (0.018 mg per day) (Tables S15, S16).

284 When age-dependent changes in weight were binned by lifespan (Figure S1), they
285 showed that heavier individuals lived longer (See Section E in Supplement). This suggests
286 that the apparent increase in average weight seen in late adult life (evidenced by a significant
287 quadratic effect of age in Table S14 and increase in weight towards the end of life in Figure 4)
288 is due to selective disappearance of lighter beetles (Effect of lifespan: $P < 0.001$).

289 For both males (Table S17, Figure 5) and females (Table S18, Figure 6), *age-*
290 *dependent mortality* (survival senescence) was affected by adult temperature (Males: $P <$
291 0.001 ; Females: $P < 0.001$), but not developmental temperature (Males: $P = 0.210$; Females:
292 $P = 0.590$), nor by an interaction between developmental and adult temperature (Males: $P =$
293 0.590 ; Females: $P = 0.820$).

294

295 Discussion

296 Early and late life environments can interact in complex ways to shape adult traits.
297 Consequently, the results of studies testing the effects of exposure to favourable or
298 unfavourable early life conditions both during the development and adulthood are mixed. To
299 improve our understanding of how heat stress experienced at different life stages affects
300 individual phenotypes, as well as to test, whether interactive effects of early and late life
301 environments affect rates of ageing, we subjected juvenile and adult *C. maculatus* to a
302 combination of stressful/hot temperatures and benign/ancestral temperatures. We then
303 measured a range of age-independent and age-dependent traits in both males and females. We

304 found that while female reproductive traits were affected negatively by stressful
305 developmental temperature, somatic traits, such as lifespan and survival senescence, were
306 affected negatively by stressful adult temperature, and weight senescence was affected by an
307 interaction between these environments.

308 We found that individuals experiencing hot/stressful temperatures during development
309 emerged sooner as adults than those experiencing ancestral temperatures, supporting the
310 metabolic theory of ecology of a faster pace of life (Clarke, 2006). However, accelerated
311 development caused by high temperatures came with costs, such as lower body weight at
312 emergence (which is well known to occur in ectotherms: Zuo et al, 2012), and lower
313 emergence success. Additionally, in females, hot developmental temperatures resulted in
314 reduced reproductive performance (lower LRS and fertility, faster reproductive senescence).
315 These results support the silver-spoon hypothesis for female reproduction, suggesting that
316 independent of the adult environment, favourable developmental environments increase
317 female fitness (see also Cooper & Kruuk, 2018; Sanghvi et al, 2021).

318 Additionally, when exposed to hot/stressful adult temperatures, females had higher
319 early adult life reproduction (on Days 1 to 3), but shorter lifespans and faster reproductive
320 senescence. These findings support classic life-history theory (Partridge 1987; Stearns, 1989)
321 which proposes a trade-off between early and late life reproduction (Reed et al, 2008), and
322 between survival and reproduction (Kirkwood & Rose, 1999; Marshall et al, 2017). However,
323 our results contrast with a previous study investigating the effects of the developmental
324 density experienced by seed beetles (Sanghvi et al 2021), which showed no effect of high
325 density on the trade-off between female early and late life reproduction, or between female
326 reproduction and survival. This suggests that trade-offs between early and late adult life traits
327 are specific to, and mediated by, the type of environmental parameter being manipulated (e.g.
328 Hammers et al, 2013). In the presence of high temperature, such trade-offs appear to be

329 common across taxa, including seed beetles (Berger et al, 2017; Kim et al, 2020). There are
 330 several potential explanations for such patterns. For example, individuals experiencing hot
 331 temperatures may adopt a “live-fast die-young” life-history strategy (Robinson et al, 2006).
 332 Here, if hot temperatures decrease expected future reproduction and survival, this would be
 333 expected to trigger females to terminally invest in early reproduction (Clutton-Brock, 1984),
 334 although this increased early life investment would lead to faster senescence in later life (e.g.
 335 Gribble et al, 2018). Alternatively, individuals exposed to cooler temperatures might show
 336 reduced survival senescence because during early adult life they allocate resources to somatic
 337 maintenance rather than reproduction (Kirkwood & Austad, 2000). It is also possible that
 338 temperature affects these traits independently, and that the correlations between survival and
 339 reproduction are non-causal.

340 Hot adult temperatures lead to lower adult lifespan and higher age-dependent mortality
 341 (survival senescence) in both males and females. The lack of a sex-specific effect on overall
 342 survival is not surprising since, again, high temperatures in ectotherms are known to affect
 343 longevity as a consequence of increased metabolism (Brown et al, 2004), which is likely to
 344 affect males and females in a similar way. More surprising, perhaps, is that the developmental
 345 environment did not also affect these somatic traits in a deleterious way. A reason for this
 346 could be that selective disappearance of poor quality individuals at the developmental stage of
 347 led to an average increase in adult lifespan in hot temperatures, especially in females (See
 348 section D in supplement for more information). Another reason may be that somatic traits are
 349 only affected by current environments, or that organisms are able to better compensate for
 350 poor somatic traits than for reproductive traits, after experiencing unfavourable developmental
 351 environments.

352 In contrast to the other traits, we found that early and late environments interacted to
 353 affect age-dependent changes in male weight. This interaction was due to the differences in

354 age-dependent decline in weight between hot and ancestral developmental temperature being
 355 greater when adult temperature are hot compared to when they are ancestral (Table S15, S16).
 356 Additionally, males who experienced hot temperature at both stages, showed a slower rate of
 357 age-dependent loss in weight (Table S15) compared to males who experienced favourable
 358 developmental but hot adult temperatures. This result is consistent with the beneficial
 359 acclimation hypothesis (Wilson & Franklin, 2002), which is a form of adaptive plasticity.
 360 Although, because the absolute differences in the rate of weight loss between males in these
 361 treatments of our study is low (only 0.049 mg per day), whether this result is biologically
 362 meaningful, remains unknown. Evidence for beneficial acclimation due to an interaction
 363 between adult and developmental environments (West-Eberhard, 2003) has been commonly
 364 found in species where temperature is manipulated (Leroi et al, 1994; Geister & Fischer,
 365 2007; Reviewed in Wilson & Franklin, 2002). However, previous studies looking at age-
 366 dependent traits have not found any evidence for beneficial acclimation effects when
 367 manipulating foraging environments (Briga et al, 2019), or diet and temperature (Min et al,
 368 2021). A testable hypothesis for why we found some evidence for beneficial acclimation
 369 could be that the allocation of resources towards somatic (i.e. body weight) maintenance, by
 370 males who experience developmental stress, occurs at the expense of investment in
 371 reproduction.

372 A recent study (Duxbury & Chapman, 2020), which aimed to test between the silver-
 373 spoon and environmental matching hypotheses, manipulated developmental and adult
 374 nutrition, and found that female reproductive senescence was affected by an interaction
 375 between developmental and adult diets. However, another study that manipulated both adult
 376 and developmental temperatures in *Drosophila* found results similar to ours (Min et al, 2020).
 377 Specifically, they found that adult temperature had a greater effect on age-dependent survival
 378 than developmental temperature, and that hot adult temperatures were deleterious for adult

379 survival senescence. However, they also found an interaction of adult and developmental
380 temperatures to affect age-dependent fecundity deleteriously, which we did not. One reason
381 why we did not find such interactions could be due to the kind of environmental variable that
382 was manipulated (temperature in our study, diet in Duxbury & Chapman, 2020) and different
383 biology of the species studied.

384 Finally, we also found two population-level patterns in senescence which could have
385 important ecological and evolutionary consequences. First, there were significant differences
386 in rates of reproductive senescence between females, as well as between families (of full-
387 sibs). This was evidenced by models which allowed the slopes of both, different females and
388 families to vary, providing a better fit to the data than models which did not. Individual-level
389 variation in senescence has been shown previously in wild animals (Bouwhuis et al, 2010),
390 and is essential for traits (in our case, reproductive senescence) to evolve via natural selection.
391 Further, the differences in rates of reproductive senescence between families suggest this trait
392 is heritable and thus able to evolve. Second, we found evidence for selective disappearance of
393 lighter males with increasing age. This may have masked individual-level decreases in weight
394 due to heavier individuals surviving longer. Such evidence of individual-level patterns of
395 senescence being masked by population patterns of ageing due to selective disappearance of
396 individuals has previously only been shown in vertebrates (Bouwhuis et al, 2009; Hayward et
397 al, 2013).

398

399 **Conclusion**

400 Ours is one of the first studies to test how heat stress experienced at different life-
401 stages interacts to affect individual life-histories and senescence. We show that depending on
402 the trait and the sex measured, either developmental, adult, or the interaction between both
403 environments can affect the resulting phenotype. This suggests that the way environments

404 affect an individual's phenotypic responses is complex and shows that each trait can follow
 405 different trajectories, providing support to different aspects and hypotheses of life-history
 406 theory. In consequence, we highlight the importance of measuring fitness-related traits
 407 throughout an organism's life, as well as measuring both physiological and life-history
 408 components of fitness in order to understand the holistic effects of environments on
 409 individuals. Considering that the adult environment might have stronger influence than
 410 developmental environments on traits which are not direct measures of reproduction, we
 411 suggest that studies should integrate the effects of early and late life environments to avoid
 412 biased results, as well as measure a diverse range of life-history and physiological traits. If
 413 traits change differently over time in different environments, it is crucial that studies measure
 414 these traits throughout the lifetime of organisms.

415

416 **References**

- 417 ADLER, M., TELFORD, M. & BONDURIANSKY, R. 2016. Phenotypes optimized for
 418 early-life reproduction exhibit faster somatic deterioration with age, revealing a latent
 419 cost of high condition. *Journal of Evolutionary Biology*, 29, 2436-2446.
- 420 BAHRNDORFF, S., GERTSEN, S., PERTOLDI, C. & KRISTENSEN, T. N. 2016.
 421 Investigating thermal acclimation effects before and after a cold shock in *Drosophila*
 422 *melanogaster* using behavioural assays. *Biological Journal of the Linnean Society*,
 423 117, 241-251.
- 424 BALBONTÍN, J. & MØLLER, A. 2015. Environmental conditions during early life
 425 accelerate the rate of senescence in a short-lived passerine bird. *Ecology*, 96, 948-
 426 959.
- 427 BATES, D., MACHLER, M., BOLKER, B. and WALKER, S., 2014. Fitting linear mixed-

428 effects models using lme4. *arXiv preprint:1406.5823*.

429 BATESON, P., GLUCKMAN, P. & HANSON, M. 2014. The biology of developmental
430 plasticity and the Predictive Adaptive Response hypothesis. *The Journal of*
431 *Physiology*, 592, 2357-2368.

432 BEAMAN, J. E., WHITE, C. R. & SEEBACHER, F. 2016. Evolution of plasticity:
433 mechanistic link between development and reversible acclimation. *Trends in Ecology*
434 *& Evolution*, 31, 237-249.

435 BECK, C. W. & BLUMER, L. S. 2011. A handbook on bean beetles, *Callosobruchus*
436 *maculatus*. National Science Foundation.

437 BERGER, D., STANGBERG, J., GRIESHOP, K., MARTINOSI, I. and ARNQVIST, G.,
438 2017. Temperature effects on life-history trade-offs, germline maintenance and
439 mutation rate under simulated climate warming. *Proceedings of the Royal Society B:*
440 *Biological Sciences*, 284, 20171721.

441 BOUWHUIS, S., CHARMANTIER, A., VERHULST, S. & SHELDON, B. C. 2010.
442 Individual variation in rates of senescence: natal origin effects and disposable soma in
443 a wild bird population. *Journal of Animal Ecology*, 79, 1251-1261.

444 BOUWHUIS, S., SHELDON, B., VERHULST, S. & CHARMANTIER, A. 2009. Great tits
445 growing old: selective disappearance and the partitioning of senescence to stages
446 within the breeding cycle. *Proceedings of the Royal Society B: Biological Sciences*,
447 276, 2769-2777.

448 BRIGA, M., JIMENO, B. & VERHULST, S. 2019. Coupling lifespan and aging? The age at
449 onset of body mass decline associates positively with sex-specific lifespan but
450 negatively with environment-specific lifespan. *Experimental Gerontology*, 119, 111-
451 119.

452 BRIGA, M., KOETSIER, E., BOONEKAMP, J. J., JIMENO, B. & VERHULST, S. 2017.
453 Food availability affects adult survival trajectories depending on early developmental
454 conditions. *Proceedings of the Royal Society B: Biological Sciences*, 284, 20162287.

455 BROWN, J.H., GILLOOLY, J.F., ALLEN, A.P., SAVAGE, V.M. & WEST, G.B., 2004.
456 Toward a metabolic theory of ecology. *Ecology*, 85, 1771-1789.

457 CEBALLOS, C.P. & VALENZUELA, N., 2011. The role of sex-specific plasticity in shaping
458 sexual dimorphism in a long-lived vertebrate, the snapping turtle *Chelydra*
459 *serpentina*. *Evolutionary Biology*, 38, 163-181.

460 CLARKE, A. 2006. Temperature and the metabolic theory of ecology. *Functional Ecology*,
461 20, 405-412.

462 CLEAL, J. K., POORE, K. R., BOULLIN, J. P., KHAN, O., CHAU, R., HAMBIDGE, O.,
463 TORRENS, C., NEWMAN, J. P., POSTON, L., NOAKES, D. E., HANSON, M. A. &
464 GREEN, L. R. 2007. Mismatched pre- and postnatal nutrition leads to cardiovascular
465 dysfunction and altered renal function in adulthood. *Proceedings of the National*
466 *Academy of Sciences*, 104, 9529-9533.

467 CLUTTON-BROCK, T. H. 1984. Reproductive Effort and Terminal Investment in
468 Iteroparous Animals. *The American Naturalist*, 123, 212-229.

469 COOPER, E. B. & KRUUK, L. E. 2018. Ageing with a silver spoon: A meta-analysis of
470 the effect of developmental environment on senescence. *Evolution Letters*, 2, 460-471.

471 DEERE, J. A. & CHOWN, S. L. 2006. Testing the beneficial acclimation hypothesis and its
472 alternatives for locomotor performance. *The American Naturalist*, 168, 630-644.

473 DESCAMPS, S., BOUTIN, S., BERTEAUX, D., MCADAM, A. G. & GAILLARD, J. M.
474 2008. Cohort effects in red squirrels: the influence of density, food abundance and
475 temperature on future survival and reproductive success. *Journal of Animal Ecology*,

476 77, 305-314.

477 DMITRIEW, C. & ROWE, L., 2007. Effects of early resource limitation and compensatory
478 growth on lifetime fitness in the ladybird beetle (*Harmonia axyridis*). *Journal of*
479 *Evolutionary Biology*, 20, 1298-1310.

480 DOUGHERTY, L. R., VAN LIESHOUT, E., MCNAMARA, K. B., MOSCHILLA, J. A.,
481 ARNQVIST, G. & SIMMONS, L. W. 2017. Sexual conflict and correlated evolution
482 between male persistence and female resistance traits in the seed beetle
483 *Callosobruchus maculatus*. *Proceedings of the Royal Society B: Biological Sciences*,
484 284, 20170132.

485 DUXBURY, E. M. L. and CHAPMAN, T. 2019. Sex-Specific responses of Life Span and
486 Fitness to Variation in Developmental Versus Adult Diets in *Drosophila*
487 *melanogaster*. *The Journals of Gerontology: Series A*, 7, 1431-1438.

488 ENGQVIST, L. 2005. The mistreatment of covariate interaction terms in linear model
489 analyses of behavioural and evolutionary ecology studies. *Animal Behaviour*, 70, 967-
490 971.

491 ENGQVIST, L. and REINHOLD, K. 2016. Adaptive trans-generational phenotypic plasticity
492 and the lack of an experimental control in reciprocal match/mismatch experiments.
493 *Methods in Ecology and Evolution*, 7, 1482-1488.

494 FOX, C. W., STILLWELL, R. C., WALLIN, W. G., CURTIS, C. L. & REED, D. H. 2011.
495 Inbreeding-environment interactions for fitness: complex relationships between
496 inbreeding depression and temperature stress in a seed-feeding beetle. *Evolutionary*
497 *Ecology*, 25, 25-43.

498 FOX, C.W., DUBLIN, L. & POLLITT, S.J. 2003. Gender differences in lifespan and
499 mortality rates in two seed beetle species. *Functional Ecology*, 17, 619-626.

500 GEISTER, T.L. & FISCHER, K., 2007. Testing the beneficial acclimation hypothesis:
501 temperature effects on mating success in a butterfly. *Behavioral Ecology*, 18, 658-664.

502 GLUCKMAN, P. D., HANSON, M. A. & SPENCER, H. G. 2005. Predictive adaptive
503 responses and human evolution. *Trends in Ecology & Evolution*, 20, 527-533.

504 GRAFEN, A. 1988. On the uses of data on lifetime reproductive success. In: Clutton-Brock,
505 T.H. (ed) Reproductive success. Chicago University Press, Chicago, pp 454-471

506 GRIBBLE, K. E., MORAN, B. M., JONES, S., COREY, E. L. & MARK WELCH, D. B.
507 2018. Congeneric variability in lifespan extension and onset of senescence suggest
508 active regulation of aging in response to low temperature. *Experimental Gerontology*,
509 114, 99-106.

510 HAMMERS, M., RICHARDSON, D., BURKE, T. & KOMDEUR, J. 2013. The impact of
511 reproductive investment and early life environmental conditions on senescence:
512 support for the disposable soma hypothesis. *Journal of Evolutionary Biology*, 26,
513 1999-2007.

514 HARTIG, F. 2020. DHARMA: Residual diagnostics for hierarchical (multi-level/mixed)
515 regression models. R Package version 0.3.2.0.<http://florianhartig.github.io/DHARMA/>

516 HARRISON, X. A. 2014. Using observation-level random effects to model overdispersion in
517 count data in ecology and evolution. *PeerJ*, 2, e616.

518 HAYWARD, A. D. & LUMMAA, V. 2013. Testing the evolutionary basis of the predictive
519 adaptive response hypothesis in a preindustrial human population. *Evolution*,
520 *Medicine, and Public Health*, 2013, 106-117.

521 HAYWARD, A. D., WILSON, A. J., PILKINGTON, J. G., CLUTTON-BROCK, T. H.,
522 PEMBERTON, J. M. & KRUUK, L. E. 2013. Reproductive senescence in female
523 Soay sheep: variation across traits and contributions of individual ageing and selective

524 disappearance. *Functional Ecology*, 27, 184-195.

525 HELLE, H., KOSKELA, E. & MAPPES, T. 2012. Life in varying environments:
526 experimental evidence for delayed effects of juvenile environment on adult life
527 history. *Journal of Animal Ecology*, 81, 573-582.

528 HOOPER, A. K., SPAGOPOULOU, F., WYLDE, Z., MAKLAKOV, A. A. &
529 BONDURIANSKY, R. 2017. Ontogenetic timing as a condition-dependent life history
530 trait: High-condition males develop quickly, peak early, and age fast. *Evolution*, 71,
531 671-685.

532 HUEY, R. B., BERRIGAN, D., GILCHRIST, G. W. & HERRON, J. C. 1999. Testing the
533 adaptive significance of acclimation: a strong inference approach. *American Zoologist*,
534 39, 323-336.

535 HUNT, J., BROOKS, R., JENNIONS, M. D., SMITH, M. J., BENTSEN, C. L. &
536 BUSSIÈRE, L. F. 2004. High-quality male field crickets invest heavily in sexual
537 display but die young. *Nature*, 432, 1024.

538 IGLESIAS-CARRASCO, M., BROOKES, S., KRUUK, L.E. & HEAD, M.L., 2020. The
539 effects of competition on fitness depend on the sex of both competitors. *Ecology and*
540 *Evolution*, 10, 9808-9826.

541 KELLERMANN, V., VAN HEERWAARDEN, B. & SGRÒ, C. M. 2017. How important is
542 thermal history? Evidence for lasting effects of developmental temperature on upper
543 thermal limits in *Drosophila melanogaster*. *Proceedings of the Royal Society B:*
544 *Biological Sciences*, 284, 20170447.

545 KIM, K.E., JANG, T. & LEE, K.P., 2020. Combined effects of temperature and
546 macronutrient balance on life-history traits in *Drosophila melanogaster*: implications
547 for life-history trade-offs and fundamental niche. *Oecologia*, 193.

548 KIRKWOOD, T. B. & AUSTAD, S. N. 2000. Why do we age? *Nature*, 408, 233.

549 KIRKWOOD, T. B. & ROSE, M. R. 1991. Evolution of senescence: late survival sacrificed
550 for reproduction. *Philosophical Transactions of the Royal Society of London*, 332, 15-
551 24.

552 KLEINTEICH, A., WILDER, S. M. & SCHNEIDER, J. M. 2015. Contributions of juvenile
553 and adult diet to the lifetime reproductive success and lifespan of a spider. *Oikos*, 124,
554 130-138.

555 KLEPSATEL, P., KNOBLOCHOVÁ, D., GIRISH, T. N., DIRCKSEN, H. & GÁLIKOVÁ,
556 M. 2020. The influence of developmental diet on reproduction and metabolism in
557 *Drosophila*. *BMC Evolutionary Biology*, 20, 93.

558 KLEPSATEL, P., GIRISH, T. N., DIRCKSEN, H. & GÁLIKOVÁ, M. 2019. Reproductive
559 fitness of *Drosophila* is maximised by optimal developmental temperature. *Journal of*
560 *Experimental Biology*, 222.

561 KRAUSE, E. T., KRÜGER, O. & SCHIELZETH, H. 2017. Long-term effects of early
562 nutrition and environmental matching on developmental and personality traits in zebra
563 finches. *Animal Behaviour*, 128, 103-115.

564 KRISTENSEN, T. N., HOFFMANN, A. A., OVERGAARD, J., SØRENSEN, J. G.,
565 HALLAS, R. & LOESCHCKE, V. 2008. Costs and benefits of cold acclimation in
566 field-released *Drosophila*. *Proceedings of the National Academy of Sciences*, 105,
567 216-221.

568 LENTH, R., SINGMANN, H., LOVE, J., BUERKNER, P., HERVE, M. 2019. Package
569 “emmeans.” CRAN v1.6.3.

570 LEROI, A.M., BENNETT, A.F. & LENSKE, R.E., 1994. Temperature acclimation and
571 competitive fitness: an experimental test of the beneficial acclimation

572 assumption. *Proceedings of the National Academy of Sciences*, 91, 1917-1921

573 MADSEN, T. & SHINE, R. 2000. Silver spoons and snake body sizes: prey availability early
574 in life influences long-term growth rates of free-ranging pythons. *Journal of Animal*
575 *Ecology*, 69, 952-958.

576 MAGNUSSON, A., SKAUG, H., NIELSEN, A., BERG, C., KRISTENSEN, K.,
577 MAECHLER, M., VAN BENTHAM, K., BOLKER, B., BROOKS, M., & BROOKS,
578 M.M. 2017. Package ‘glmmTMB’. *R Package V 0.2. 0*.

579 MAKLAKOV, A. A., HALL, M. D., SIMPSON, S. J., DESSMANN, J., CLISSOLD, F. J.,
580 ZAJITSCHKE, F., LAILVAUX, S. P., RAUBENHEIMER, D., BONDURIANSKY,
581 R. & BROOKS, R. C. 2009. Sex differences in nutrient-dependent reproductive
582 ageing. *Aging Cell*, 8, 324-30.

583 MARAIS, E. & CHOWN, S.L., 2008. Beneficial acclimation and the Bogert effect. *Ecology*
584 *Letters*, 11, 1027-1036.

585 MARSHALL, H. H., VITIKAINEN, E. I., MWANGUHYA, F., BUSINGE, R.,
586 KYABULIMA, S., HARES, M. C., INZANI, E., KALEMA-ZIKUSOKA, G.,
587 MWESIGE, K. & NICHOLS, H. J. 2017. Lifetime fitness consequences of early-life
588 ecological hardship in a wild mammal population. *Ecology and Evolution*, 7, 1712-
589 1724.

590 METCALFE, N. B., and P. MONAGHAN. 2001. Compensation for a bad start: grow now,
591 pay later? *Trends in Ecology & Evolution*, 16, 254–260.

592 MIN, K.W., JANG, T. and LEE, K.P. 2020. Thermal and nutritional environments during
593 development exert different effects on adult reproductive success in *Drosophila*
594 *melanogaster*. *Ecology and evolution*, 11, 443-457.

595 MONAGHAN, P. 2008. Early growth conditions, phenotypic development and environmental

596 change. *Philosophical Transactions of the Royal Society of London B: Biological*
597 *Sciences*, 363, 1635-1645.

598 MÜLLER, T., KÜLL, C. L. & MÜLLER, C. 2016. Effects of larval versus adult density
599 conditions on reproduction and behavior of a leaf beetle. *Behavioral Ecology and*
600 *Sociobiology*, 70, 2081-2091.

601 NAKAGAWA, S., CUTHILL, I.C. 2007. Effect size, confidence intervals and statistical
602 significance: a practical guide for biologists. *Biological Reviews of the Cambridge*
603 *Philosophical Society*, 82, 591-605.

604 NUSSEY, D. H., KRUUK, L. E., MORRIS, A. & CLUTTON-BROCK, T. H. 2007.
605 Environmental conditions in early life influence ageing rates in a wild population of
606 red deer. *Current Biology*, 17, R1000-R1001.

607 PARTRIDGE, L. 1987. Is Accelerated Senescence a Cost of Reproduction? *Functional*
608 *Ecology*, 1, 317-320.

609 PARTRIDGE, L., & SILBY, R. 1991. Constraints in the evolution of life histories.
610 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 332, 3–13

611 PIGEON, G., LOE, L. E., BISCHOF, R., BONENFANT, C., FORCHHAMMER, M.,
612 IRVINE, R. J., ROPSTAD, E., STIEN, A., VEIBERG, V. & ALBON, S. 2019. Silver
613 spoon effects are constrained under extreme adult environmental conditions. *Ecology*,
614 100, e02886.

615 R DEVELOPMENT CORE TEAM, R. 2011. R: A language and environment for statistical
616 computing. R foundation for statistical computing Vienna, Austria.

617 REED, T. E., KRUUK, L. E., WANLESS, S., FREDERIKSEN, M., CUNNINGHAM, E. J. &
618 HARRIS, M. P. 2008. Reproductive senescence in a long-lived seabird: rates of
619 decline in late-life performance are associated with varying costs of early

620 reproduction. *The American Naturalist*, 171, E89-E101.

621 ROBINSON, M.R., PILKINGTON, J.G., CLUTTON-BROCK, T.H., PEMBERTON, J.M.

622 & KRUK, L.E., 2006. Live fast, die young: trade-offs between fitness components

623 and sexually antagonistic selection on weaponry in Soay sheep. *Evolution*, 60, 2168-

624 2181.

625 ROSE, M. & CHARLESWORTH, B. 2002. A test of evolutionary theories of senescence.

626 *Science's SAGE KE*, 2002, 17.

627 SANTOS, M. A., CARROMEU-SANTOS, A., QUINA, A. S., SANTOS, M., MATOS, M. &

628 SIMÕES, P. 2021. High developmental temperature leads to low reproduction despite

629 adult temperature. *Journal of Thermal Biology*, 95, p.102794

630 SANGHVI, K., ZAJITSCHKE, F., IGLESIAS-CARRASCO, M., HEAD, M. J. 2021. Sex-

631 and trait-specific silver-spoon effects of developmental environments, on ageing.

632 *Evolutionary Ecology*, **35**, 367–385.

633 SCHARF, I., BRAF, H., IFRACH, N., ROSENSTEIN, S., SUBACH, A. 2015. The Effects of

634 Temperature and Diet during Development, Adulthood, and Mating on Reproduction

635 in the Red Flour Beetle. *PLoS ONE*, 10(9), e0136924.

636 SCHARF, I., GALKIN, N. & HALLE, S. 2015. Disentangling the consequences of growth

637 temperature and adult acclimation temperature on starvation and thermal tolerance in

638 the red flour beetle. *Evolutionary Biology*, 42, 54-62.

639 SCOTT, G. R. & JOHNSTON, I. A. 2012. Temperature during embryonic development has

640 persistent effects on thermal acclimation capacity in zebrafish. *Proceedings of the*

641 *National Academy of Sciences*, 109, 14247.

642 SPAGOPOULOU, F., TEPLITSKY, C., LIND, M. I., GUSTAFSSON, L. & MAKRAKOV,

643 A. 2019. Silver-spoon upbringing improves early-life fitness but promotes

644 reproductive ageing in a wild bird. *Ecology Letters*, 23, 994-1002.

645 STEARNS, S. C. 1989. Trade-offs in life-history evolution. *Functional Ecology*, 3, 259-268.

646 STILLWELL, R. C., BLANCKENHORN, W., TEDER, T., DAVIDOWITZ, G., FOX, C. W.

647 2010. Sex Differences in Phenotypic Plasticity Affect Variation in Sexual Size

648 Dimorphism in Insects: From Physiology to Evolution. *Annual Review of Entomology*,

649 **55**, 227-245.

650 STILLWELL, R. C. & FOX, C. W. 2005. Complex patterns of phenotypic plasticity:

651 interactive effects of temperature during rearing and oviposition. *Ecology*, 86, 924-

652 934.

653 STILLWELL, R. C., WALLIN, W. G., HITCHCOCK, L. J. & FOX, C. W. 2007. Phenotypic

654 plasticity in a complex world: interactive effects of food and temperature on fitness

655 components of a seed beetle. *Oecologia*, 153, 309-321.

656 TABORSKY, B. 2006. The influence of juvenile and adult environments on life-history

657 trajectories. *Proceedings of the Royal Society B: Biological Sciences*, 273, 741-750.

658 THERNEAU, T. 2014. Coxme: Mixed-effects Cox models. R v 2.2-16. [https://cran.r-](https://cran.r-project.org/web/packages/coxme/index.html)

659 [project.org/web/packages/coxme/index.html](https://cran.r-project.org/web/packages/coxme/index.html)

660 VAN DE POL, M., BRUINZEEL, L. W., HEG, D., VAN DER JEUGD, H. P. &

661 VERHULST, S. 2006. A silver spoon for a golden future: long-term effects of natal

662 origin on fitness prospects of oystercatchers (*Haematopus ostralegus*). *Journal of*

663 *Animal Ecology*, 75, 616-626.

664 VAN DE POL, M., & VERHULST, S. 2006. Age-dependent traits: A new statistical model to

665 separate within- and between- individual effects. *American Naturalist*, 167, 766-773

666 VASUDEVA, R., DEEMING, D. C. & EADY, P. E. 2014. Developmental temperature

667 affects the expression of ejaculatory traits and the outcome of sperm competition in

668 *Callosobruchus maculatus*. *Journal of Evolutionary Biology*, 27, 1811-8.

- 669 WEST-EBERHARD, M. J. 2003. *Developmental plasticity and evolution*, Oxford University
670 Press.
- 671 WILSON, R. S. & FRANKLIN, C. E. 2002. Testing the beneficial acclimation hypothesis.
672 *Trends in Ecology & Evolution*, 17, 66-70.
- 673 WONG, J. W. & KÖLLIKER, M. 2014. Effects of food restriction across stages of juvenile
674 and early adult development on body weight, survival and adult life history. *Journal of*
675 *Evolutionary Biology*, 27, 2420-2430.
- 676 WOODS, H. A. & HARRISON, J. F. 2002. Interpreting rejections of the beneficial
677 acclimation hypothesis: when is physiological plasticity adaptive? *Evolution*, 56,
678 1863-1866.
- 679 ZAJITSCHKE, F., HUNT, J., JENNIONS, M.D., HALL, M.D. & BROOKS, R.C. 2009.
680 Effects of juvenile and adult diet on ageing and reproductive effort of male and female
681 black field crickets, *Teleogryllus commodus*. *Functional Ecology*, 23, 602-611.
- 682 ZUO, W., MOSES, M. E., WEST, G. B., HOU, C. & BROWN, J. H. 2012. A general model
683 for effects of temperature on ectotherm ontogenetic growth and development.
684 *Proceedings of the Royal Society B: Biological Sciences*, 279, 1840-1846.

685 Table 1. Summary of traits and models used for analyses. DevT. =Developmental temperature, AdultT. =Adult temperature, Age= Adult age

Trait	Definition	Model type	Error distribution	Data Transformaton (LMM) / Link Function (GLMM)	Fixed effects	Random Effects
Emergence success	Likelihood of adults emerging from a bean with an egg laid on it	GLMM	Binomial	Logit	DevT. + Block	Family
Development time	Number of days between the laying of an egg, and the emergence of an adult	LMM	Gaussian	Power $((y^\lambda - 1)/\lambda)$ Males: $\lambda = -0.133214$ Females: $\lambda = 0.2275$	DevT. + Block	Family
Emergence weight	Weight (mg) of beetle on the day of emergence	LMM	Gaussian	Males: None Females: None	DevT. + Block	Family
Adult lifespan	Number of days between the emergence of an individual and its death	LMM	Gaussian	Males: None Females: Log _e (y)	DevT. * AdultT. + Emergence weight + Block	Family
Fertility (females)	Likelihood that a female laid at least one egg in her lifetime	GLM	Binomial	Logit	DevT. * AdultT. + Block	None
Life time reproductive success (females)	LRS: total number of eggs laid by a female in her lifetime	GLMM	Poisson	Log _e (y)	DevT. * AdultT. + Adult Lifespan + Block	Family, Observation
Age dependent (daily) fecundity (females)	Number of eggs laid by a female each day, measured since day of emergence throughout her lifespan	GLMM	Negative binomial distribution	Log _e (y)	DevT. * AdultT. * Age (and Age ²) + Adult Lifespan + Block	Family, Individual ID (and additional models with Age Family and/or Age ID as random

						effects)
Age- dependent weight (males)	Weight (mg) of males measured every alternate day, since day of emergence, throughout his lifespan	LMM	Gaussian	None	DevT. * AdultT. * Age (and Age^2) + Age*Emergence weight + Adult Lifespan + Block	Family, Individual ID
Age- dependent survival	Likelihood of adult beetles dying at a given adult age	Cox- Proportion al hazards		None	DevT.* AdultT. + Block	Family

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695 Table 2. Summary of results for effects of developmental and adult temperatures on all measured traits (ns: $P > 0.05$). DevT =Developmental
696 temperature, AdultT= Adult temperature, A= Ancestral temperature, H= Hot temperature, Age= Adult age.

Trait	DevT		AdultT		DevT* AdultT		DevT*Age	AdultT*Age	DevT*AdultT*Age
	males	females	males	females	males	females			
Emergence success (both sexes)	H < A								
Development time	H < A	H < A							
Emergence weight	H < A	H < A							
Adult lifespan	H > A	H > A	H < A	H < A	ns	ns			
Female fertility		H < A		ns		ns			
Female LRS		H < A		H < A		ns			
Female age-dependent (daily) fecundity		-		-		-	Yes	Yes	ns
Male age-dependent adult weight	-		-		-		Yes	-	Yes
Age-dependent survival	ns	ns	Yes	Yes	ns	ns			

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699 Figure 1. The effects of developmental and adult temperatures on female (red) and male

700 (blue) adult lifespan. *Ancestral developmental and ancestral adult (AA), ancestral*

701 *developmental and hot adult (AH), hot developmental and hot adult (HH), and hot*

702 *developmental and ancestral adult (HA) temperatures. Median, interquartile ranges (25,50,*

703 *75%) and upper and lower extremes presented.*

Figure 2. Violin plot comparing the smoothed probability density, median, interquartile ranges (25,50, 75%), and upper and lower extremes presented. of the effects of developmental and adult temperature on female lifetime reproductive success (LRS). *Ancestral developmental and ancestral adult (AA)*, *ancestral developmental and hot adult (AH)*, *hot developmental and hot adult (HH)*, and *hot developmental and ancestral adult (HA)* temperatures. Letters ‘a to c’ denote significant differences between pairwise comparisons of groups, with same letters denoting no significant difference.

Figure 3. Effects of adult age on female daily fecundity for all four treatments: *Ancestral developmental and ancestral adult (AA-Purple)*, *ancestral developmental and hot adult (AH-Green)*, *hot developmental and hot adult (HH-Orange)*, and *hot developmental and ancestral adult (HA-Red)* temperatures. Shaded regions represent 95% confidence intervals.

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718 Figure 4. Effects of adult age on weight (mg) in males for all four treatments of: *Ancestral*
 719 *developmental and ancestral adult (AA-Purple)*, *ancestral developmental and hot adult (AH-*
 720 *Green)*, *hot developmental and hot adult (HH-Orange)*, and *hot developmental and ancestral*
 721 *adult (HA-Red)* temperatures. Shaded regions represent 95% confidence intervals.

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725 Figure 5. The survival probability of adult males from four treatments with increasing age,
 726 namely: *Ancestral developmental and ancestral adult (AA-red)*, *ancestral developmental and*
 727 *hot adult (AH-green)*, *hot developmental and hot adult (HH-purple)*, and *hot developmental*

728 and ancestral adult (**HA-blue**) temperatures, using Kaplan-Meier curves. Shaded regions
729 represent 95% confidence intervals.

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732 Figure 6. The survival probability of adult females from four treatments with increasing age,
733 namely: *Ancestral developmental and ancestral adult (AA-red)*, *ancestral developmental and*
734 *hot adult (AH-green)*, *hot developmental and hot adult (HH-purple)*, and *hot developmental*
735 *and ancestral adult (HA-blue)* temperatures, using Kaplan-Meier curves. Shaded regions
736 represent 95% confidence intervals.