Environmental variation mediates the evolution of anticipatory parental effects

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Abstract

Environments vary over time and if this variation is predictable, environments that are similar across generations should favour evolution of anticipatory parental effects to benefit offspring. In contrast, the absence of correlation between parental and offspring environments should select against parental effects. However, experimental evidence is scarce. We investigated the evolution of maternal effects using experimental evolution. Populations of the nematode *Caenorhabditis remanei*, adapted to 20°C, were exposed to a novel temperature (25°C) for 30 generations with either positive or zero correlation between parent and offspring temperature. We found that populations evolving in environments with positive correlations had a positive maternal effect, since they required maternal exposure to 25°C to achieve maximum reproduction and fitness in 25°C. In contrast, populations evolving under zero correlation had lost this positive maternal effect. This shows that parental effects can aid population viability in warming environments. Correspondingly, ill-fitting parental effects can be rapidly lost.

Key words: *Caenorhabditis*, Environmental heterogeneity, Maternal effects, Reproduction, Temperature, Transgenerational plasticity

Introduction

The role of environmental variation in the adaptive expression of phenotypes has gathered considerable interest (Chevin *et al.* 2010; Hollander *et al.* 2015; Donelson *et al.* 2017; Lind & Spagopoulou 2018). Not only is heterogeneity common, it is also predicted to change evolutionary outcomes. While stable environments generally should select for genetic specialisation, environmental heterogeneity can select for environmental input on this process. Variable environments is expected to select for phenotypic plasticity (if environmental cues are reliable) or bet-hedging (if the cues are not reliable) (Moran 1992; Simons 2011). However, a developing organism may not be able to acquire and/or interpret the environmental cues itself; therefore, the parental environment can also function as a developmental cue (Marshall & Uller 2007; Leimar & McNamara 2015). Consequently, recent theory maintains that high environmental correlation between generations can select for adaptive parental effects and/or epigenetic inheritance of an environmentally induced phenotype (Lachmann & Jablonka 1996; Bonduriansky & Day 2009; Rivoire & Leibler 2014; Kuijper & Hoyle 2015; Leimar & McNamara 2015; Uller *et al.* 2015; Proulx & Teotónio 2017), mechanisms collectively referred to as transgenerational plasticity (Donelson *et al.* 2017). The sign of the environmental correlation is expected to result in a similar sign of the parental effect, so that parents can prepare their offspring for the same environment as they are themselves experiencing (positive correlation), the opposite environment (negative correlation) or does not influence the phenotype of their offspring (zero correlation between parent and offspring environments). The exception is constant (perfectly correlated) environments, where genetic specialisation is predicted to evolve (Leimar & McNamara 2015) together with a negative trans-

generational effect in order to reduce phenotypic variance (Hoyle & Ezard 2012; Kuijper & Hoyle 2015).

However, while the theory is well developed, the empirical evidence is mixed. In its most basic form, the theory of anticipatory parental effects predicts that offspring should have higher performance if parental and offspring environments are matching (Marshall & Uller 2007; Burgess & Marshall 2014). There are some striking examples of this (e.g. Gustafsson *et al.* 2005; Galloway & Etterson 2007; Jensen *et al.* 2014; Kishimoto *et al.* 2017; Ryu *et al.* 2018; Toyota *et al.* 2019), but across studies there is only weak support for this prediction in natural systems, and the effects are small compared to the direct effects of offspring environment (reviewed in Uller *et al.* 2013). Since environmental predictability across generations is seldom quantified, one reason for the scarcity of clear examples of adaptive parental effects is that environments may not often be correlated across generations, and, therefore, provide little opportunity for selection for such anticipatory effects (Burgess & Marshall 2014). Even if natural environments are correlated, the evidence for stronger parental effects in more stable environments is mixed, and varies between traits (Walsh *et al.* 2016). Thus, there is a call for studies estimating parent and offspring fitness when the environmental predictability between generations are well known, and maternal effects are expected to be under selection (Burgess & Marshall 2014).

Direct experimental evidence for the evolution of positive anticipatory parental effects of an environmentally induced parental phenotype is currently lacking. On the other hand, if parents and offspring live in negatively correlated environments, the parental phenotype should not be inherited, but the parents can still anticipate the offspring

environment. As such, the evolution of a negative parental effect could be adaptive, a prediction that has recently received experimental support in a study by Dey *et al.* (Dey *et al.* 2016), who found that populations of the nematode *Caenorhabditis elegans* that evolved under strictly alternating hypoxia-normoxia conditions in every generation evolved a negative maternal provisioning effect. This suggests an adaptive benefit of maternal effects when the maternal environment is a strong cue for the offspring environment (in this case a perfect negative correlation), as predicted by theory (Uller *et al.* 2015; Proulx & Teotónio 2017). More generally, theory also predicts that positive trans-generational correlations would result in the evolution of a positive parental effect and, importantly, if the environmental state is uncorrelated across generations, parental effects would be maladaptive and selected against (Lachmann & Jablonka 1996; Kuijper & Hoyle 2015; Leimar & McNamara 2015; Uller *et al.* 2015). The latter is considered a reason why adaptive parental effects are generally weak (Uller *et al.* 2013). However, these scenarios have not been investigated experimentally. Moreover, previous studies on evolution of parental effects under environmental heterogeneity have investigated only the case of non-overlapping generations (Dey *et al.* 2016). Most natural populations have however overlapping generations and age structure, which can influence evolution in both stable and heterogeneous environments, especially with respect to the evolution of life history strategies (Cotto & Ronce 2014).

Taken together, environmental heterogeneity and environmental correlations over generations predict the adaptive value of parental effects (Lachmann & Jablonka 1996; Kuijper & Hoyle 2015; Uller *et al.* 2015). We set out to test this using experimental evolution in the dioecious free-living nematode *Caenorhabditis*

118 *remanei*, adapting to different temperature regimes. Genetically heterogeneous
119 populations, previously adapted to 20°C, were evolving for 30 generations in control
120 conditions or adapting to 25°C, in either constant 25°C, increased warming to 25°C or
121 a heterogeneous environment with fluctuating temperatures. We found positive
122 anticipatory maternal effects on reproduction in populations evolving in environments
123 that were positively correlated across generations. Moreover, we found the evolution
124 of a reduced maternal effect on reproduction in heterogeneous environments where
125 parent and offspring environments were not correlated during experimental evolution.
126

127 **Material and methods**

128

129 *Experimental evolution*

130 As founder population, we used the wild-type SP8 strain of *C. remanei*, obtained from
131 N. Timmermeyer at the Department of Biology, University of Tübingen, Germany.
132 This strain was created by crossing three wild-type isolates of *C. remanei* (SB146,
133 MY31, and PB206), harbour substantial standing genetic variation for life-history
134 traits (Chen & Maklakov 2012; Lind *et al.* 2017), and has been lab-adapted to 20°C
135 for 15 generations prior to setup of experimental evolution.

136 Experimental evolution was conducted for 30 generations in three climate cabinets;
137 one set to 20°C, one to 25°C and one with a slowly increasing temperature (see
138 below). Five selection regimes were used. *Control 20°C* was experiencing 20°C for
139 30 generations, and *Warm 25°C* was experiencing 25°C for 30 generations. *Increased*
140 *warming* started in 20°C, the cabinet temperature was then raised by 0.1°C every 2.13
141 day (rounded to whole days) to reach 25°C the last day of selection. *Slow temperature*
142 *cycles* spend their first 10 generations in 20°C, were then moved to the 25°C cabinet

143 for 10 generations, to finish the last 10 generations in the 20°C cabinet. Finally, the
144 *Fast temperature cycles* regime were moved between 20°C and 25°C every second
145 generation, thus experiencing 15 temperature shifts.

146 Generation time in 20°C and 25°C was defined as the average difference in age
147 between parents and offspring (Charlesworth 1994) and was calculated from the life-
148 table of age-specific reproduction and survival by solving the Euler-Lotka equation
149 (Stearns 1992; Charlesworth 1994) with trial data from the SP8 lines, and was 4.0
150 days in 20°C and 3.4 days in 25°C. This resulted 120 days of selection for *Control*
151 *20°C*, 114 days for *Slow temperature cycles*, 110 days for *Increased warming* and
152 *Fast temperature cycles* and 101 days for *Warm 25°C*. For the two temperature cycle
153 treatments, the worms spent shorter chronological time in 25°C than in 20°C, because
154 of the faster generation time in 25°C. This ensured equal exposure to the two
155 temperatures over biological time.

156 Experimental evolution was conducted on 92 mm NGM-plates (Stiernagle 2006) and
157 to combat infections the agar and bacterial LB also contained the antibiotics
158 kanamycin and streptomycin, and the fungicide nystatin (Lionaki & Tavernarakis
159 2013; Lind *et al.* 2016). The plates were seeded with 2mL of the antibiotic resistant *E.*
160 *coli* strain OP50-1 (pUC4K) obtained from J. Ewbank at the Centre d'Immunologie
161 de Marseille- Luminy, France. To keep worm populations age-structured in
162 overlapping generations, the lines were always kept in experimental growth face by
163 cutting out a bit of agar containing 150 individuals of mixed ages and transferring this
164 to freshly seeded plates. Transfer was conducted when needed (every 1-2 day), always
165 before food was finished. Six independent replicate populations of each selection
166 treatment were set up, resulting in a total of 30 populations. All populations were

167 expanded for two generations and frozen after 30 generations.

168

169 *Phenotypic assays*

170 Before assays, worms were recover from freezing and grown 2 generations in
171 common garden, each generation synchronized by bleaching, a standard procedure
172 that kills all life-stages but eggs (Stiernagle 2006). The common garden temperature
173 was 20°C or 25°C (see below).

174

175 Fitness assays were performed to test for local adaptation to the selective regime and
176 the evolution of adaptive trans-generational effects. We therefore carried out three
177 assays, by varying parental temperature (the 2 generations of common garden after
178 defrosting the lines) and testing temperature for offspring. The *20°C - 20°C assay* had
179 both common garden and testing in 20°C. This is the environment the *Control 20°C*
180 lines have experienced. Likewise, in the *25°C - 25°C assay* both parents and testing
181 worms experience 25°C, which is the selective environment for *Warm 25°C* and very
182 close to the final environment for *Increased warming*. Finally, the *20°C - 25°C assay*
183 have 20°C as parental temperature, while the testing worms have their whole
184 development in 25°C. This assay represents strong temperature fluctuations between
185 generations, which is the selective environments for the *Fast temperature cycle* lines,
186 and by comparing this assay to the *25°C - 25°C assay* we can estimate the importance
187 of trans-generational effects on fitness when adapting to a novel environment.

188

189 The assays were initiated by synchronised egg-laying in the testing temperature by 40
190 females of each population. After 5h, females were killed by bleaching, and setup of

L4 larvae was initiated 39h later (in 25°C) or 50h later (in 20°C), due to temperature-specific development time. The setup consisted of 8 testing females per plate, together with the same number of background males from the SP8 line. Sex ratio was kept 1:1 throughout the experiment by adjusting the number of males to match the number of females alive. Age-specific fecundity was measured by each day allowing the females 3h of egg-laying on an empty plate, where after the females were returned to a new plate (together with the males) and the number of hatched offspring on the egg-laying plate were counted 2 days later. The exact time the females were added to and removed from each plate was noted, and the number of offspring was corrected by exact number of minutes available for egg laying, and the number of females alive. Thus, we did not collect individual level data on total reproduction, but daily snapshot, in order to increase the number of individuals assayed and improve the reproduction estimate of each population. Daily reproduction was collected until all reproduction had ceased. Four replicate plates of each population was set up, and for the *20°C - 20°C* and *20°C - 25°C* assays the replicates were evenly split between two climate cabinets per temperature. However, for logistical reasons, the *20°C - 25°C assay* was reduced. We excluded the *Slow temperature cycle* treatment from this assay, and unfortunately we lost two *Warm 25°C* populations during common garden (due to overcrowding and subsequent starving, which is known to induce epigenetic effects (Rechavi *et al.* 2014) and therefore these populations were excluded), leaving us with 4 replicate population of this treatment. This resulted in 30 replicate populations and 960 female worms for the *20°C - 20°C* and *20°C - 25°C* assays, and 23 replicate populations and 736 female worms for the *25°C - 25°C assay*.

Statistical analyses

The age-specific reproduction data was analysed as rate-sensitive individual fitness λ_{ind} (Brommer *et al.* 2002) as well as the total reproduction of each replicate plate, adjusted to the number of females present each day. Individual fitness encompasses the timing and number of offspring and is analogous to the intrinsic rate of population growth (Stearns 1992) and was calculated by solving the Euler-Lotka equation for each replicate plate. Individual fitness and total reproduction in 20°C was analysed in separate mixed effect models with election treatment as fixed effect and population and cabinet as random effects. Both response variables were log-transformed before analysis. In 25°C, individual fitness and total reproduction was analysed with selection treatment and parental temperature as crossed fixed effects, and replicate population as random effect. Since the *25°C - 25°C assay* was conducted in only one cabinet, and moreover the *Slow temperature cycle* treatment was not run, the random effect of cabinet was excluded from the models, as was the *Slow temperature cycle* treatment.

Results

For individual fitness (λ_{ind}) in 25°C, we found a significant selection regime × parental temperature interaction (Selection regime: $\chi^2 = 1.302$, df = 3, p = 0.729; Parental temperature: $\chi^2 = 0.114$, df = 1, p = 0.736, Selection regime × Parental temperature: $\chi^2 = 15.562$, df = 3, p = 0.001). This interaction was caused by significantly opposite slope for *Fast temperature cycles* compared to *Increased warming* and *Warm 25°C*, with highest fitness in 25°C for *Fast temperature cycles*

when parents were grown in 20°C, while highest fitness in 25°C for *Increased warming* and *Warm 25°C* was achieved when their parents were also grown in 25°C (Figure 1A).

A significant selection regime × parental temperature interaction was also found for total reproduction in 25°C (Selection regime: $\chi^2 = 0.995$, df = 3, p = 0.802; Parental temperature: $\chi^2 = 41.373$, df = 1, p < 0.001, Selection regime × Parental temperature: $\chi^2 = 10.747$, df = 3, p = 0.013), caused by a much weaker positive effect of parental exposure to 25°C for *Fast temperature cycles* than for the other selection regimes (Figure 1B). Finally, we found a fitness cost of adaptation, since all lines had reduced individual fitness (λ_{ind}) in 20°C relative to the *Control 20°C* lines ($\chi^2 = 19.799$, df = 4, p < 0.001, Figure 2). The cost was however not detected in total reproduction ($\chi^2 = 2.238$, df = 4, p = 0.692, Supplementary figure 1).

Discussion

The degree of environmental variation can influence the expression of phenotypes (Moran 1992; Uller *et al.* 2015; Proulx & Teotónio 2017). In addition to genetic specialisation, the phenotype can match the environment either by phenotypic plasticity, where the offspring matches its development to the current environment, or by anticipatory parental effects, where the offspring non-genetically inherit the parents phenotype to match its environment, thus improving offspring performance if parent and offspring environments are matching (Marshall & Uller 2007; Donelson *et al.* 2017). While within-generation phenotypic plasticity is common (DeWitt &

266 Scheiner 2004), parental effects seem, in contrast, to be generally weak (Uller *et al.*
267 2013), despite some well known examples (Gustafsson *et al.* 2005; Galloway &
268 Etterson 2007; Jensen *et al.* 2014; Kishimoto *et al.* 2017; Ryu *et al.* 2018; Toyota *et*
269 *al.* 2019). Since trans-generational effects should evolve only if there is a strong
270 correlation between parent and offspring environments (Kuijper & Hoyle 2015;
271 Leimar & McNamara 2015; Uller *et al.* 2015), it is possible that environments
272 generally are not highly correlated between generations, thus explaining why such
273 anticipatory effects are uncommon (Uller *et al.* 2013). However, the environmental
274 predictability is seldom investigated in studies of parental effects (Burgess &
275 Marshall 2014). Therefore, we investigated whether the degree of temporal
276 environmental variation, as well as the correlation between parent and offspring
277 environment, influenced the evolution of maternal effects.
278
279 We found that the presence of environmental variation mediated the evolution of
280 maternal effects on reproduction and individual fitness (λ_{ind}) in *C. remanei* nematode
281 worms adapting to a novel and stressful warm temperature (25°C) for 30 generations
282 (see predictions and findings summarized in Supplementary table 1). For all
283 populations evolving in stable or slowly increasing temperature (*Control 20°C*, *Warm*
284 *25°C*, *Increased warming*), a strong positive maternal effect on reproductive output
285 resulted in an increased offspring production in 25°C when the parents were also
286 cultured in 25°C and not in 20°C. Since these populations have evolved in
287 environments with high and positive environmental correlations over generations,
288 trans-generational effects are adaptive and predicted by theory (Mousseau & Fox
289 1998; Kuijper & Hoyle 2015; Leimar & McNamara 2015; Uller *et al.* 2015). This
290 result is also in agreement with a recent study by Dey *et al.* (2016) who found the

evolution of an anticipatory negative maternal effect in *C. elegans* evolving in perfectly negatively correlated environments. Our finding of positive anticipatory maternal effects in positively correlated environments highlights the importance of experimental evolution studies with known environmental correlations to study the evolution of adaptive trans-generational effects.

In contrast to environments with high positive correlations, the *Fast temperature cycles* populations evolved in a fluctuating environment where the temperature changed every second generation. Thus, the next generation would with equal likelihood be exposed to the same or a different temperature as the parents, resulting in zero correlation between parent and offspring environments. In this environment, trans-generational effects are not considered adaptive (Mousseau & Fox 1998; Uller *et al.* 2015), and, in agreement with the theory, we found a loss of the positive maternal effect, since the reproductive output in 25°C of these lines was independent of the environment their parents. The adaptive value of these differences in parental effects is illustrated in the individual fitness (λ_{ind}) of the different selection treatments. *Fast temperature cycles* populations had highest λ_{ind} in 25°C only when the parents were cultured for two generations in 20°C, a situation mimicking the fluctuating environments they were exposed to during evolution. Although adaptive, this should be defined as negative maternal on λ_{ind}, which is not predicted by theory. Thus, maternal effects on reproduction and λ_{ind} does not follow the same pattern for the *Fast temperature cycles*, but importantly, none of the measures show the positive maternal effects present in lines from more positively correlated environments (figure 1). In contrast, populations adapting to more or less stable warm temperatures (*Warm 25°C* and *Increased warming*) improved λ_{ind} when parents were also cultured in 25°C,

316 which mimics stable temperatures over generations and a positive maternal effect on
317 λ_{ind}. Whether the negative maternal effect on fitness in the *Fast temperature cycles* is
318 a result of the fact that the assays with parents and offspring in 25°C represent a
319 stability not experienced evolutionary by the *Fast temperature cycles* populations
320 (two generations common garden for the parents and one generation offspring testing
321 equals to three generations in the same environment), or is a general response when
322 parent and offspring environment is not matching is unknown.
323
324 In addition, we also found a fitness cost of adaptation, since all populations evolving
325 in new environments had lower λ_{ind} in the original environment (20°C), compared to
326 the *Control 20°C* populations. Moreover, although *Control 20°C* showed a positive
327 maternal effect on reproduction, parental exposure to 25°C did not improve their
328 individual fitness, suggesting that an evolutionary history in 25°C is needed for
329 maximum fitness in this temperature.
330
331 While the positive maternal effect present in both stable (*Control 20°C*, *Warm 25°C*)
332 and slowly increasing (*Increased warming*) temperature regimes is anticipated when
333 there is positive autocorrelation between parent and offspring environments
334 (Lachmann & Jablonka 1996; Uller *et al.* 2015), perfectly stable environments are
335 actually predicted to select for negative trans-generational effects (Hoyle & Ezard
336 2012; Kuijper & Hoyle 2015). When a population is well adapted to a stable
337 optimum, a negative maternal effect reduces phenotypic variance between
338 generations. However, we find no support for this prediction, since both treatments in
339 stable environments (*Control 20°C*, *Warm 25°C*) showed a positive maternal effect,
340 even after 30 generations in stable conditions. It is however possible that these lines

still show transient dynamics, since a positive trans-generational effect is predicted to evolve as a transient response when experiencing a novel environment (Kuijper & Hoyle 2015), in a similar way to how phenotypic plasticity is predicted to aid adaptation to new environments (Price *et al.* 2003; Lande 2009; Chevin *et al.* 2010; Coulson *et al.* 2017). It could possibly be argued that the positive trans-generational effect is non-adaptive, caused by the lines being maladapted in 20°C and therefore producing low-quality offspring in this temperature. However, the fact that the *Control 20°C* lines, who have highest fitness in 20°C and who have not experienced 25°C for at least 45 generations show positive maternal effects on reproduction of parental exposure to 25°C argues against a non-adaptive explanation and instead reinforces the view that all lines from stable and slowly changing environment has an adaptive positive maternal effect. In agreement with this, exposing a laboratory strain of *C. elegans* to 25°C (Schott *et al.* 2014) or to starvation (Rechavi *et al.* 2014) results in heritable changes in gene expression, directed by inherited small RNA (Rechavi *et al.* 2014; Schott *et al.* 2014; Houri-Zeevi & Rechavi 2017), which further suggests that transgenerational plasticity such as maternal effects and epigenetic inheritance is important in *Caenorhabditis* nematodes.

We found that the environmental correlation between generations is driving the evolution of anticipatory maternal effects, and the experimental design assured low within-generation heterogeneity. While stable and slowly changing environments select for positive anticipatory maternal effects, environments that fluctuate with no correlation between generations select against parental influence on offspring phenotype. This is the first empirical study that investigates the evolutionary loss of anticipatory maternal effect, which follow theoretical predictions (Kuijper & Hoyle

366 2015; Uller *et al.* 2015) and suggest that one reason for the weak effects of parent
367 environment on offspring phenotype in natural systems (Uller *et al.* 2013) could be
368 that natural environments are not always temporally correlated across generations.
369 While most examples of positive parental effects comes from systems with short life-
370 cycles such as nematodes (Kishimoto *et al.* 2017), daphniids (Gustafsson *et al.* 2005;
371 Toyota *et al.* 2019), annelids (Jensen *et al.* 2014) and herbs (Galloway & Etterson
372 2007), it is also been found in fish where the generation time span years (Ryu *et al.*
373 2018). However, when investigating maternal effects in *Daphnia* from natural
374 populations with different degree of variation in predation intensity, Walsh *et al.*
375 (2016) found some support for stronger positive maternal effects in population from
376 more stable environments, but the effect differed between traits and no effect was
377 found on reproduction. Nevertheless, these types of studies where the environmental
378 predictability is known are vital for our understanding of the selection pressures
379 resulting in the presence or absence of adaptive maternal effects in natural populations
380 (Burgess & Marshall 2014), where deconstruction of environmental predictability to
381 seasonality and environmental colour noise (following Marshall & Burgess 2015) is a
382 very promising approach.
383
384 On-going climate change is not only resulting in warmer temperatures, but also
385 increased temperature variation, which can impact both the ecology and evolution of
386 populations and species (Vasseur *et al.* 2014; Vázquez *et al.* 2017), and trans-
387 generational acclimation can be an important response to deal with a warming climate
388 (Donelson *et al.* 2017; Ryu *et al.* 2018). We show that environmental heterogeneity
389 drives the evolution of maternal effects, and support the theoretical predictions
390 (Lachmann & Jablonka 1996; Uller *et al.* 2015) that the correlation between parent

and offspring environment is the driver of the evolution of transgenerational plasticity.

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Competing interests

The authors report no competing interests.

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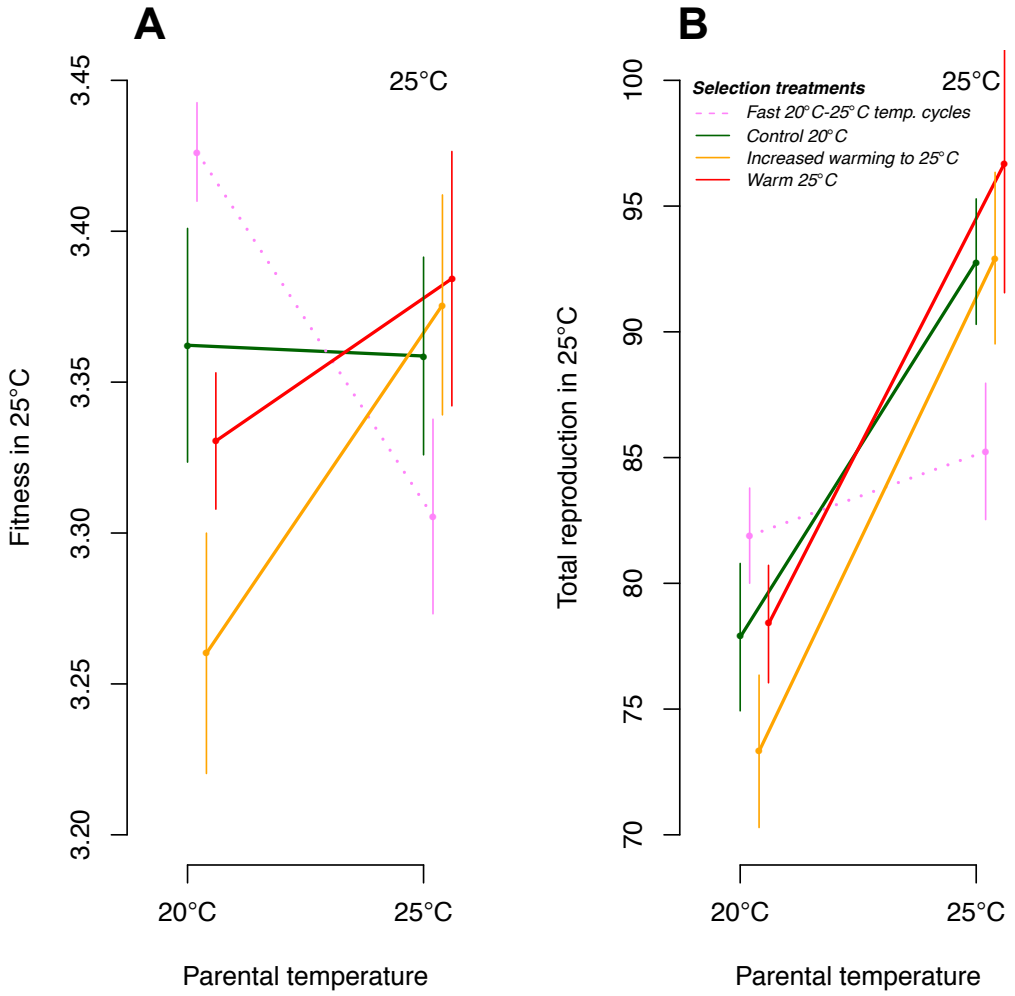

Figure 1. The effect of parental temperature on fitness and reproduction in 25°C. Individual fitness λ_{ind} (A) and total reproduction (B) in 25°C when parent were raised for 2 generations in either 20°C or 25°C. Symbols represent selection treatments (mean ± SE). *Control 20°C* and *Warm 25°C* have spent 30 generations in 20°C or 25°C, respectively. *Increased warming* has been subjected to slowly increased temperatures, starting in 20°C and reaching 25°C at generation 30. *Fast temperature* cycles have spent two generations in 20°C, followed by two generations in 25°C, this cycle has then been repeated for 30 generations.

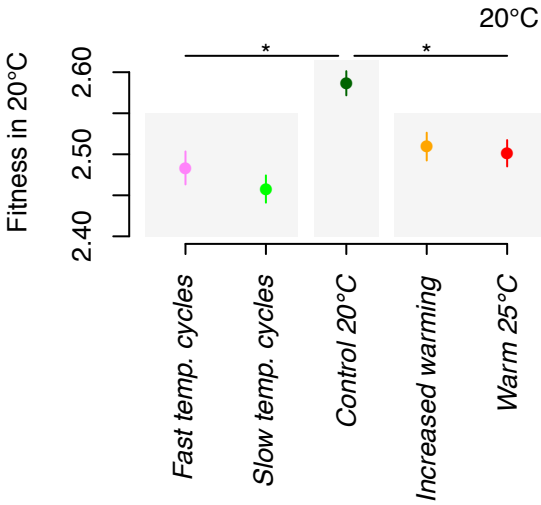

Figure 2. Fitness in original environment. Individual fitness λ_{ind} in 20°C when parents are also grown for two generations in 20°C. Symbols represent selection treatments (mean ± SE). Grey symbolises treatments groups that differ significantly in fitness.