

1 **Title: The effect of sexual selection on adaptation and extinction under**
2 **increasing temperatures**

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11 Running Head: Sexual selection and climate change

12 **Abstract**

13 Strong sexual selection has been reported to both enhance and hinder the adaptive capacity
14 and persistence of populations when exposed to novel environments. Consequently, how
15 sexual selection influences population adaption and persistence under stress remains widely
16 debated. Here we present two empirical investigations of the fitness consequences of sexual
17 selection on populations of the Indian meal moth, *Plodia interpunctella*, exposed to stable or
18 gradually increasing temperatures. When faced with increasing temperatures strong sexual
19 selection was associated with both increased fecundity and offspring survival compared to
20 populations experiencing weak sexual selection, suggesting sexual selection acts to drive
21 adaptive evolution by favouring beneficial alleles. Strong sexual selection did not, however,
22 delay extinction when the temperature became excessively high. By manipulating
23 individuals' mating opportunities during fitness assays we were able to assess the effect of
24 multiple mating independently from the effect of population-level sexual selection, and found
25 that polyandry has a positive effect on both fecundity and offspring survival under increasing
26 temperatures in those populations evolving with weak sexual selection. Within stable
27 temperatures there were some benefits from strong sexual selection but these were not
28 consistent across the entire experiment, possibly reflecting changing costs and benefits of
29 sexual selection under stabilising and directional selection. These results indicate that sexual
30 selection can provide a buffer against climate change and increase adaptation rates within a
31 continuously changing environment. These positive effects of sexual selection may however
32 be too small to protect populations and delay extinction when environmental changes are
33 relatively rapid.

34 **Keywords:** sexual selection, climate change, adaption, extinction, increasing temperature,
35 polyandry

36 **Introduction**

37 Some models of global climate change predict increases of over 4°C in mean global
38 temperature within the next century with associated increases in extreme weather events [1].
39 The impact of climate change on ecosystems and biodiversity remains difficult to predict but
40 it is certain that many species across the globe will be affected. Adaptation to environmental
41 change can occur via phenotypic plasticity or genetic change [2] but the degree of plasticity
42 available in most populations is likely to be limited and in most cases some degree of genetic
43 change via natural selection will be necessary to allow persistence. Despite recent attempts to
44 understand adaption and extinction risk during environmental change [3], it has been
45 highlighted that our current understanding of the underlying mechanisms which influence the
46 adaptive capacity and vulnerability of species is poor [4,5]. One such poorly understood
47 mechanism with broad implications is the effect of sexual selection on adaptation rates and
48 extinction risk (reviewed in 6,7).

49 Sexual selection is ubiquitous in sexually reproducing organisms, caused by competition
50 between individuals over access to copulations and fertilizations, and it is a potent
51 evolutionary force responsible for many of the more dramatic traits found in nature [8,9].
52 There are varying costs and benefits to individual fitness associated with sexual selection
53 leading to considerable debate regarding the overall effect sexual selection could have on
54 population viability [6,10–16] and its potential implications for applied conservation and
55 biodiversity management [17–20]. One potentially important beneficial effect of sexual
56 selection on populations is caused by ‘good genes’ mechanisms of sexual selection which
57 can, theoretically, increase adaptation rates [15,16].

58 There is growing evidence that in many cases mating success appears to be based upon the
59 condition-dependence of sexually selected traits which themselves reflect the underlying

60 genetic quality of the bearer via the ‘genic capture’ mechanism [21–24]. In these systems
61 sexual selection can influence mean population fitness by skewing reproductive success in
62 favour of males with more beneficial alleles and/or fewer deleterious mutations than the
63 overall population average [11–13]. These effects are likely to be especially important during
64 environmental change: Lorch et al. [15] proposed that those individuals most suited to the
65 new environment will have the greatest expression of condition-dependent sexually selected
66 traits, skewing reproductive success in their favour. As a consequence of the increased
67 reproductive success experienced by these ‘high quality’ males, sexual selection can increase
68 the proportion of alternative beneficial alleles in a population and enhance adaptation rates to
69 novel and changing environments [15,16]. Recent laboratory work has provided support for
70 these ideas, with populations of seed beetles, *Callosobruchus maculatus*, reared on a novel diet
71 [25] and flour beetles, *Tribolium castaneum*, exposed to a pesticide [26] showing reduced
72 adaptation rates when sexual selection was experimentally removed. Additionally,
73 monogamous populations of bulb mites, *Rhizoglyphus robini*, had decreased fitness and a
74 greater tendency to go extinct compared to polygamous populations when exposed to a raised
75 temperature [27]. Similarly, strong sexual selection has been shown to lead to faster removal
76 of experimentally induced deleterious mutations [28] (but also see [29,30]) and to reduce
77 extinction rates when populations are inbred, as seen in *R. robini* [31] and *T. castaneum* [32].
78 In contrast to these positive effects of sexual selection, field studies have tended to find
79 different patterns, with two studies indicating that increased sexual selection could increase
80 extinction rates [17,33]. This could arise from the high costs of sexually selected traits [10] or
81 because sexual selection reduces effective population sizes and therefore potentially genetic
82 diversity via genetic drift and increased inbreeding [14]. Furthermore, recent modelling work
83 suggests that small populations may be at higher risk of extinction when sexual selection is
84 strong due to increased risk of demographic stochasticity [16] providing a possible

85 explanation for the association between increased extinction rates and sexual selection
86 observed in the field [17,33] Finally, a number of laboratory studies have shown that sexual
87 conflict may retard the adaptive capacity of populations because traits favoured by male
88 reproductive success act antagonistically to female fitness reducing the overall viability of a
89 population [34–37].

90 All previous experimental work has used step changes in an environmental factor to explore
91 the influence of sexual selection on adaptation rates [25–27,34–36,38]. Many of the most
92 important changes in the environment today, however, are directional, with continuous
93 change happening across many generations [1,39]. Continuous environmental change
94 imposes a rather different selective environment to that experienced by a population exposed
95 to a step change in its environment. In the latter case selection will initially be directional but
96 as the population adapts selection will become stabilising. In the case of continuous
97 environmental change, however, there will be persistent lag between the phenotypic optimum
98 and the environmental variable, and selection will always be directional in nature. With a step
99 environmental change, alleles which give a selective benefit when environmental change
100 happens will continue to be selected for as the population adapts unless new genetic variants
101 or combinations which give an even closer fit to the new environment arise in the population.
102 With continuous change, alleles which give a selective benefit when the environment begins
103 to change might lose their selective advantage when further change happens, and population
104 persistence will be more dependent on the rate of creation of new genetic variants and
105 combinations than in the case of step environmental change [3,40]. Given these differences,
106 whether sexual selection will affect adaptation under directional change in the same way as
107 under a step change is not clear. Martínez-Ruiz and Knell [16] modelled the effect of
108 continuous environmental change and found that sexual selection did lead to enhanced
109 population persistence, possibly even more so than when a step change was modelled,

110 although it should be noted that the purpose of this model was not to compare these
111 environmental scenarios.

112 We describe a set of experiments to test the role of sexual selection on adaptation to gradual,
113 directional environmental change using a widely used model species, the Indian meal moth,
114 *Plodia interpunctella*. Female choice and sperm competition are both likely to be important
115 components of sexual selection in *P. interpunctella*. There is also the potential for inter-locus
116 sexual conflict to occur (see Supplementary material) and evidence for intra-locus sexual in a
117 number of shared life history traits [41]. Our experiments set out to test the effects of strong
118 and weak sexual selection on population fitness under both stabilising and directional natural
119 selection, with populations exposed to stable temperatures in one experiment and to gradually
120 increasing temperatures in the other experiment. To gain further insight into the phenotypic
121 effects of sexual selection on individual female fitness, during fitness assays in both
122 experiments we manipulated the mating system to remove or allow sexual selection, by
123 enforcing monogamy or allowing mate choice, polyandry and consequently any potential
124 inter-locus sexual conflict, respectively.

125 **Method**

126 Sixteen replicate populations were established from a large outbred laboratory population of
127 *P. interpunctella* and allocated either to a strong sexual selection treatment, with a male
128 biased sex ratio (MB; 3 males: 1 female) or to a weak sexual selection treatment, with a
129 female biased sex ratio (FB; 1 male: 3 females). Each population was also assigned to either
130 the stable temperature experiment (27°C) or to the increasing temperature experiment, in
131 which the temperature was increased by 2°C every other generation starting from 27°C (i.e.
132 $F_{1+2} = 27^{\circ}\text{C}$, $F_{2+3} = 29^{\circ}\text{C}$, etc.). The stable and increasing temperature experiments consisted
133 of 8 populations in total, 4 MB and 4 FB each.

134 In both experiments a set of fitness assays were performed every generation from F_3 onwards
135 and were carried out at the temperature currently experienced by the population within their
136 respective experiment. The fitness assays measured total female fecundity and by using a
137 subset of eggs, proportion offspring survival. The longevity of all male and female adult
138 moths used during these assays was also recorded. During fitness assays an extra treatment
139 was included to investigate phenotypic effects of sexual selection on individual female
140 fitness. In both the stable and increasing temperature experiments moths from both strong
141 and weak sexual selection treatments (MB and FB, respectively) were randomly assigned to
142 either monogamous (1 male: 1 female) or polyandrous (3 males: 1 female) mating system
143 treatments (see Supplementary method and Figure S1 for further details).

144 Statistical analysis was performed using mixed effects models with population as a random
145 effect to account for repeated measures within and between generations. The same analysis
146 was performed for both datasets from the stable and increasing temperature experiments,
147 unless stated otherwise. Direct comparisons between the temperature experiments should be
148 made with caution as statistical analysis was carried out within and not between temperature
149 experiments. Generalised linear mixed effects models with Poisson and binomial error
150 structures were fitted to the fecundity and offspring survival data, respectively. To account
151 for overdispersion in these models an observation level random effect was also included.

152 Standard linear mixed effects models were fitted to longevity data, which was log
153 transformed to reduce heteroscedasticity. Due to extremely low offspring survival in
154 generation F_8 in the increasing temperature experiment, analysis was performed on F_{3-7} only
155 for these data. Generation was fitted as a factor rather than a continuous explanatory variable
156 because exploratory analysis demonstrated that it was difficult to fit curves which gave a
157 good fit to these data without using rather complex nonlinear models. Because generation
158 was fitted as a factor temperature was not used as an explanatory variable in the increasing

159 temperature experiment. In all models sexual selection treatment (MB or FB), mating system
160 treatment (monogamy or polyandry) and generation, plus interaction terms up to the third
161 order were used as explanatory variables. To account for pseudoreplication of male longevity
162 from polyandrous mating system treatments an extra random effect of vial number was
163 included in analyses of male longevity (see Supplementary method for further details).

164 **Results**

165 *Increasing temperature experiment*

166 All populations experiencing an increasing temperature became extinct when the temperature
167 reached 35°C at generation 9. There was no effect of the strength of sexual selection on
168 population persistence in the face of increasing temperatures, indicated by a non-significant
169 interaction between sexual selection treatment and generation ($\chi^2 = 12.27$, $df = 1$, $p = 0.140$;
170 Figure S2, Table S1 and Supplementary method). The strength of sexual selection did,
171 however, have significant effects on both fecundity and offspring survival before population
172 extinction.

173 The minimal adequate model fitted to the offspring survival data retained the two-way
174 interaction between sexual selection treatment (MB or FB) and mating system treatment
175 (monogamy or polyandry: $\chi^2 = 6.2$, $df = 1$, $p = 0.013$; Figure 1a; Table S2). Additionally, the
176 main effect of generation was also retained ($\chi^2 = 220.25$, $df = 1$, $p < 0.001$). The latter arises
177 from a clear effect of increasing temperature (as indicated by generation) in reducing
178 offspring survival, with survival rates also depending on both the sexual selection and mating
179 system treatments. When monogamous mating was enforced during the fitness assays, MB
180 (stronger sexual selection) populations showed consistently higher offspring survival than FB
181 (weaker sexual selection) populations, with survival being on average 8% higher. This effect
182 was especially noticeable in the first generation after a temperature increase (figure 1a).

183 When polyandrous mating was allowed in the fitness assays this effect was not seen and
184 offspring from both FB and MB lines had survival that was comparable to that of MB
185 offspring in the enforced monogamy treatment. Weak sexual selection thus led to decreased
186 offspring survival, but only when females were not allowed to select their mates.

187 The minimal adequate model fitted to the fecundity data showed similar effects, retaining
188 both the two-way interactions between sexual selection and mating system treatments ($\chi^2 =$
189 3.88, $df = 1$, $p = 0.049$; Figure 1b; Table S2) and mating system and generation ($\chi^2 = 13.08$,
190 $df = 1$, $p = 0.023$). Under enforced monogamy MB females consistently had a higher
191 fecundity compared to FB females, laying 32 more eggs each on average. Allowing
192 polyandry during fitness assays tended to increase the fecundity of FB females and the
193 observed difference in MB and FB fecundity when under enforced monogamy largely
194 disappeared. Inspection of figure 1b and model summary indicates that the interaction
195 between mating system treatment and generation is largely driven by polyandrous females
196 having increased fecundity in generation F₈ only, and therefore no overall meaningful pattern
197 can be discerned. Upon further inspection however, fecundity was reduced by increasing
198 temperature (as indicated by generation), but only once temperatures were increased by 6°C
199 in generations F₇ and F₈.

200 Female longevity decreased throughout the experiment, indicated by a main effect of
201 generation ($\chi^2 = 250.49$, $df = 1$, $p < 0.001$; Figure 1c; Table S2). Furthermore, female
202 longevity was notably reduced by strong sexual selection, with females from MB populations
203 living for approximately 1 day less than those from FB populations ($\chi^2 = 64.27$, $df = 1$, $p <$
204 0.001). Mating system had a similar effect on female longevity and females exposed to a
205 polyandrous mating system also lived for approximately 1 day less than monogamous
206 females ($\chi^2 = 90.55$, $df = 1$, $p < 0.001$).

207 Male longevity also tended to decrease throughout the experiment. Overall, the polyandrous
208 mating system treatment significantly reduced male longevity compared to males under
209 enforced monogamy ($\chi^2 = 5.65$, $df = 1$, $p = 0.018$; Figure 1d; Table S2). A significant two-
210 way interaction between generation and sexual selection treatment was also retained in the
211 minimal adequate model ($\chi^2 = 26.86$, $df = 1$, $p < 0.001$), suggesting that the sexual selection
212 treatment influences male longevity. This interaction seems largely to arise from differences
213 between individual generations however, making general patterns hard to discern from the
214 fitted model.

215 *Stable temperature experiment*

216 When temperatures were stable throughout the experiment, the minimal adequate model
217 fitted to offspring survival data retained a significant two-way interaction between the sexual
218 selection treatment and generation ($\chi^2 = 26.47$, $df = 1$, $p < 0.001$; Figure 2a; Table S3). This
219 two-way interaction arises because although there were differences in the survival of MB and
220 FB offspring between generations, these differences were not consistent across the entire
221 experiment. In contrast, having the opportunity for mate choice and multiple mating within
222 the polyandrous mating system treatment tends to increase offspring survival ($\chi^2 = 5.91$, $df =$
223 1 , $p = 0.015$). Across the entire experiment polyandrous females had, on average, a 7% higher
224 offspring survival compared to females forced to mate monogamously.

225 Fecundity was influenced by the mating system treatment, with polyandrous females having
226 increased fecundity in a number of generations ($F_{5, 7 \& 8}$), indicated by a two-way interaction
227 between mating system and generation ($\chi^2 = 14.75$, $df = 1$, $p = 0.012$; Figure 2b; Table S3).
228 There was no effect of sexual selection treatment on female fecundity ($\chi^2 = 0.01$, $df = 1$, $p =$
229 0.952).

230 Female longevity decreased during the last three generations of the experiment ($\chi^2 = 161.58$,
231 $df = 1$, $p < 0.001$; Figure 2c; Table S3). There was a significant main effect of mating system
232 treatment, females from polyandrous mating systems tended to live for approximately 1 day
233 less than monogamous females ($\chi^2 = 69.56$, $df = 1$, $p < 0.001$). There was no effect of sexual
234 selection treatment on female longevity ($\chi^2 = 0.36$, $df = 1$, $p = 0.546$).

235 There was also a general trend for male longevity to decrease in the latter half of the
236 experiment. The significant two-way interaction between generation and sexual selection
237 treatment was retained in the minimal adequate model ($\chi^2 = 21.43$, $df = 1$, $p < 0.001$; Figure
238 2d; Table S3) and largely driven by differences within generations, meaning general patterns
239 are difficult to discern. Male longevity was also reduced by the polyandrous mating system in
240 comparison to the longevity of males under enforced monogamy ($\chi^2 = 21.68$, $df = 1$, $p <$
241 0.001).

242 **Discussion**

243 Increasing the temperature decreased the viability and the overall production of *P.*
244 *interpunctella* populations, mainly as a consequence of decreased offspring survival and
245 reduced egg production. These decreases in offspring survival and fecundity were, however,
246 reduced in the strong sexual selection treatment compared to the weak sexual selection
247 treatment, but only when monogamy was enforced during mating assays. When females from
248 these lines were assayed in a polyandrous mating system, allowing female choice and
249 competition between males, these effects were not seen: females from populations which
250 experienced weak sexual selection showed similar fecundity and offspring survival to those
251 from strong sexual selection treatments. When temperatures were stable, females who were
252 allowed polyandrous mating showed higher offspring survival, but there was no consistent
253 effect associated with the strength of sexual selection that the populations experienced.

254 The results from females assayed with enforced monogamy suggest that sexual selection is
255 acting to enhance the promotion of beneficial alleles within a population and facilitate
256 adaptation to increasing temperatures through ‘good genes’ mechanisms of sexual selection.
257 This indicates that when the environment changes continuously sexual selection can provide
258 similar benefits to those found by previous empirical studies which examined the effect of
259 sexual selection on adaptation when the environment undergoes a step change [25–27]. In
260 this case, however, the improved fitness associated with strong sexual selection was not
261 sufficient to delay extinction as temperatures continuously increased.

262 We did not directly assess the strength of condition dependence of sexually selected traits,
263 but we did find that males placed in a polyandrous mating system during fitness assays
264 experienced reduced longevity to those in monogamous conditions. Sexual selection is
265 known to be costly to males and has been shown experimentally to reduce male longevity in a
266 number of taxa (e.g. [42–44]); these costs are likely to increase with the presence of rivals
267 [45,46] and possibly explain the observed reductions in male longevity. Costly traits are
268 expected to be condition-dependent [21] and the genic capture model offers a probable
269 mechanism to explain the observed increase in offspring survival and female fecundity in
270 those populations exposed to increasing temperatures.

271 By contrast with the increasing temperature experiment, there was no consistent effect of
272 strong sexual selection in the stable temperature experiment. This could be because the
273 benefits of sexual selection are small and hard to detect in populations close to their adaptive
274 peaks, or alternatively, any benefits of sexual selection could be outweighed by the cost
275 imposed through sexual conflict and a similar finding to a number of previous experiments
276 [25,47]. This latter explanation is possible since intra-locus sexual conflict within *P.*
277 *interpunctella* is known to occur [41].

278 The difference between the assays conducted on females experiencing enforced monogamy
279 and those in a polyandrous mating system is striking, particularly in those populations
280 evolving with weak sexual selection. The increased offspring survival associated with
281 polyandry is potentially due to females being able to choose to mate with males of ‘higher’
282 quality. The increased fecundity in polyandrous females appears to be related to changes in
283 reproductive allocation [48]. Across both experiments polyandrous females tended to have an
284 increased egg laying rate over the first 96 hours of their lives (Figure S3 and S4, Table S2
285 and S3 and Supplementary method) which appears to be at the expense of longevity. *P.*
286 *interpunctella* adults do not feed and it appears that they are following a ‘live fast, die young’
287 strategy: when allowed to choose a mate they appear to be investing more resources in
288 reproduction than when monogamy is enforced, leading to higher reproductive output
289 concentrated in a shorter life. Alternatively, polyandry might provide insemination
290 advantages by increasing the genetic compatibility of gametes [49], or polyandrous females
291 might be able to derive some form of nutritional benefit from the ejaculate of multiple males
292 [50].

293 In the increasing temperature experiment, there was no apparent fitness benefit from
294 polyandry in the strong sexual selection lines. It is possible that this is because selection led
295 to all the males in these lines having higher fitness because “low quality” males would have
296 reduced reproductive success in these lines by comparison with the weak sexual selection
297 lines. Alternatively, it is possible that the males in these lines were also being selected for
298 greater competitive ability, reducing the likelihood of a female mating with the “best” male
299 from a group: if selection in these lines enabled males to acquire matings via harassment or
300 similar means then this might negate the benefits arising from polyandry. These results
301 highlight a potentially important effect which has largely been overlooked by previous
302 experimental designs: evolved and phenotypic effects of both sexual selection and sexual

303 conflict are likely to be acting and dependent on each other, and it is only because we
304 manipulated sexual selection at both the population and individual level that this came to
305 light. Had we only used a monandrous mating system in the fitness assays then the picture
306 would have been much simpler, but we would not have uncovered this more subtle and
307 complex set of effects.

308 As population sizes are reduced by increasing temperatures there will be a corresponding
309 reduction in population genetic diversity and increased inbreeding, potentially causing
310 populations to enter an extinction vortex [51]. In contrast to Plesnar-Bielak et al. [27] the
311 positive evolutionary effects of strong sexual selection in the present study were unable to
312 delay this process and the persistent increases in temperature drove all populations to
313 extinction at a similar rate. This indicates that the rate of temperature increase was greater
314 than the critical rate of environmental change [4] and that even with strong sexual selection
315 adaptation was not swift enough to enhance survival. Worryingly the rate of increase of
316 temperature in this experiment is comparable to those which longer-lived species with slow
317 generation times are predicted to experience under climate change [1].

318 If the temperature increases were halted at $\sim 31^{\circ}\text{C}$ or if the rate of temperature increase was
319 reduced strong sexual selection might have delayed the extinction of MB populations, for two
320 reasons. Firstly, we observed evolutionary effects of strong sexual selection increasing both
321 female fecundity and offspring viability at increasing temperatures, suggesting that
322 adaptation was indeed occurring faster within MB populations; and secondly, there are direct
323 and indirect benefits of polyandry within the increasing temperature experiment. Given that
324 females from MB populations are generally polyandrous, whereas females from FB
325 populations are likely to only mate once [52], the observed benefits of polyandry would on
326 average be more pronounced in populations under strong sexual selection. Understanding

327 how variation in sexual fitness is effected by differing rates and degrees of environmental
328 change remain important areas for future studies to address [6].

329 Overall, using experimental evolution we have shown clear positive evolutionary effects of
330 strong sexual selection when populations are exposed to increasing temperatures. These
331 benefits did not, however, delay the extinction of populations exposed to increasing
332 temperatures, the lack of effect might be due to the relatively large and often increases in
333 temperature. Additionally, we find a strong effect of polyandry on individual female fitness,
334 especially within increasing temperatures. This strongly suggests that benefits of female
335 choice and multiple mating may provide a buffer against and increase a population's
336 resilience to changing environments and climate change. We suggest that the degree of
337 polyandry and strength of sexual selection should be a consideration in applied conservation
338 and for those working to negate the impacts of climate change on biodiversity, especially
339 when assessing potential impacts on a range of species with differing mating systems.

340

341 **Data accessibility.** Data can be found in Supplementary material

342 **Competing interests.** We have no competing interests to declare.

343 **Authors' contributions.** RK developed original concept, JP and RK designed experiment
344 and JP performed data collection, JP and RK analysed data and wrote manuscript.

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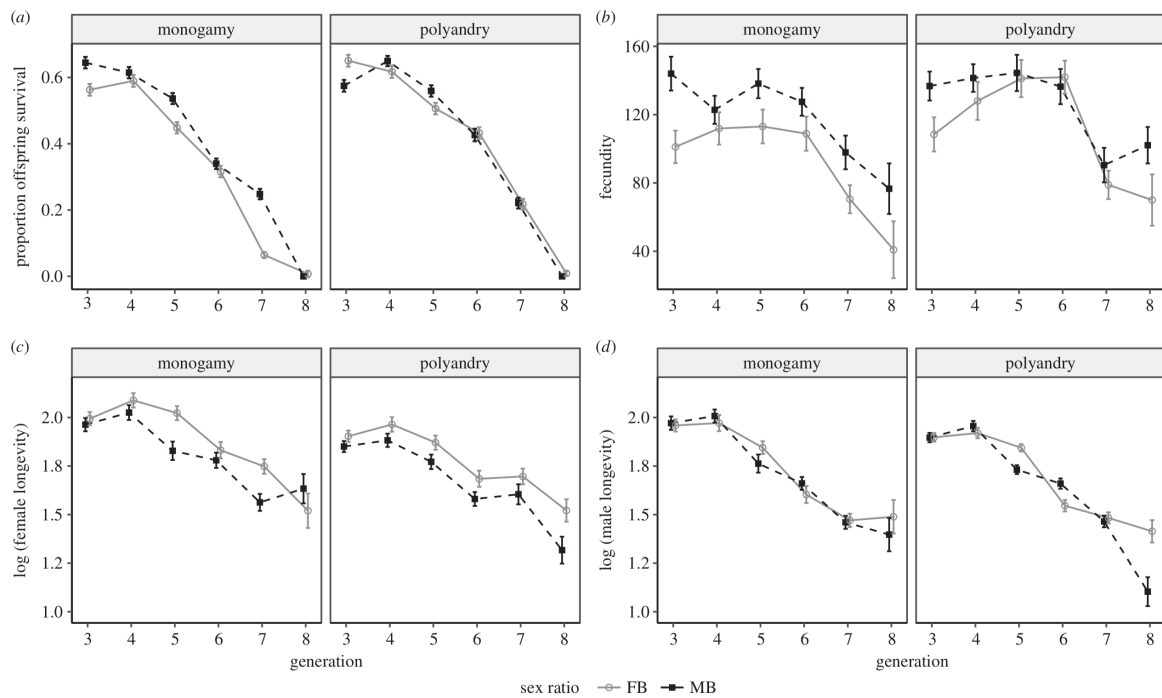
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495 **Figure 1.** Comparisons of the effect of sexual selection (MB or FB) and mating system

496 (monogamy or polyandry) treatments on a) proportion offspring survival, b) female

497 lifetime fecundity, c) log transformed female longevity and d) log transformed male

498 longevity from the increasing temperature experiment across F₃₋₈. Weak sexual

499 selection (FB) is indicated by light grey hollow circles and solid lines and strong

500 sexual selection (MB) indicated by dark grey solid squares and dashed lines. Males

501 and females placed within monogamous or polyandrous mating systems during fitness

502 assays are shown in the left and right panels, respectively. Error bars indicated

503 standard error.

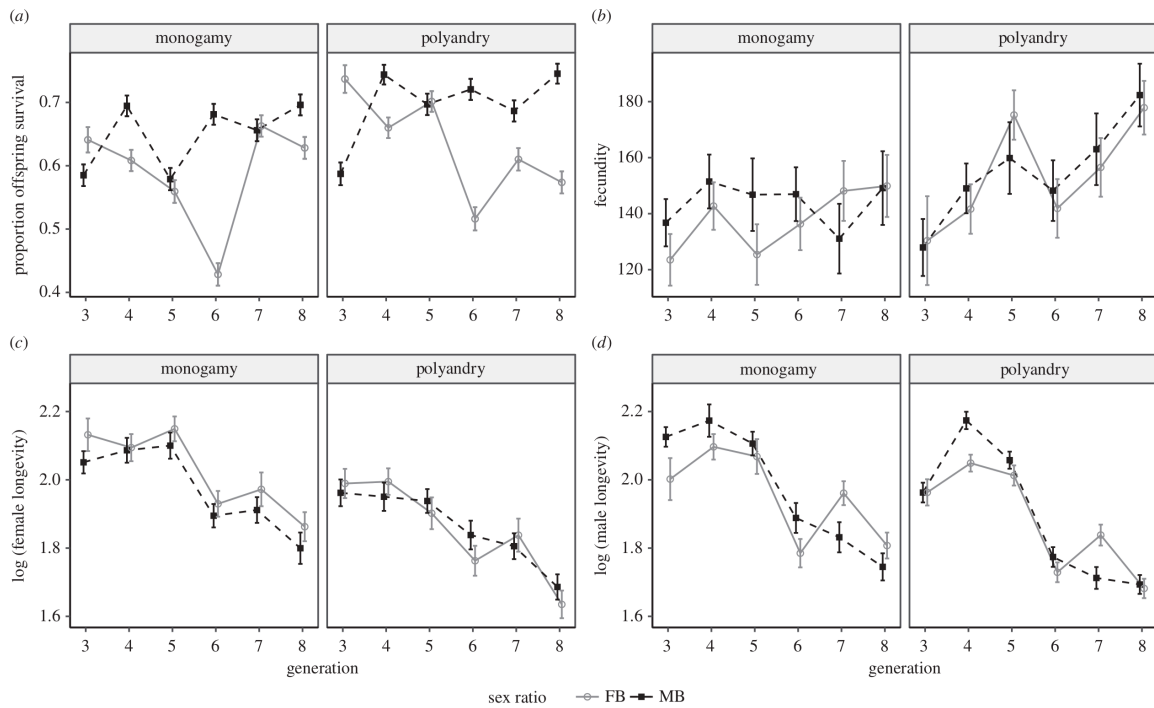
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510 **Figure 2.** Comparisons of the effect of sexual selection (MB or FB) and mating system
 511 (monogamy or polyandry) treatments on a) proportion offspring survival, b) female
 512 lifetime fecundity, c) log transformed female longevity and d) log transformed male
 513 longevity from the stable temperature experiment across F₃₋₈. Weak sexual selection
 514 (FB) is indicated by light grey hollow circles and solid lines and strong sexual
 515 selection (MB) indicated by dark grey solid squares and dashed lines. Males and
 516 females placed within monogamous or polyandrous mating systems during fitness
 517 assays are shown in the left and right panels, respectively. Error bars indicated
 518 standard error.

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