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

Introduction

Some models of global climate change predict increases of over 4°C in mean global

temperature within the next century with associated increases in extreme weather events [1].

The impact of climate change on ecosystems and biodiversity remains difficult to predict but

it is certain that many species across the globe will be affected. Adaptation to environmental

change can occur via phenotypic plasticity or genetic change [2] but the degree of plasticity

available in most populations is likely to be limited and in most cases some degree of genetic

change via natural selection will be necessary to allow persistence. Despite recent attempts to

understand adaption and extinction risk during environmental change [3], it has been

highlighted that our current understanding of the underlying mechanisms which influence the

adaptive capacity and vulnerability of species is poor [4,5]. One such poorly understood

mechanism with broad implications is the effect of sexual selection on adaptation rates and

extinction risk (reviewed in 6,7).

Sexual selection is ubiquitous in sexually reproducing organisms, caused by competition

between individuals over access to copulations and fertilizations, and it is a potent

evolutionary force responsible for many of the more dramatic traits found in nature [8,9].

There are varying costs and benefits to individual fitness associated with sexual selection

leading to considerable debate regarding the overall effect sexual selection could have on

population viability [6,10–16] and its potential implications for applied conservation and

biodiversity management [17–20]. One potentially important beneficial effect of sexual

selection on populations is caused by 'good genes' mechanisms of sexual selection which

can, theoretically, increase adaptation rates [15,16].

There is growing evidence that in many cases mating success appears to be based upon the

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    $F_{1+2} = 27°C$, $F_{2+3} = 29°C$, 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 is 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 (χ^2 =

189   3.88, df = 1, p = 0.049; Figure 1b; Table S2) and mating system and generation (χ^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 F_8 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 F_7 and F_8.

200   Female longevity decreased throughout the experiment, indicated by a main effect of

201   generation (χ^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 (χ^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 (χ^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 (χ^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 (χ^2 = 69.56, df = 1, p < 0.001). There was no effect of sexual

234   selection treatment on female longevity (χ^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 (χ^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 (χ^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 ~31°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

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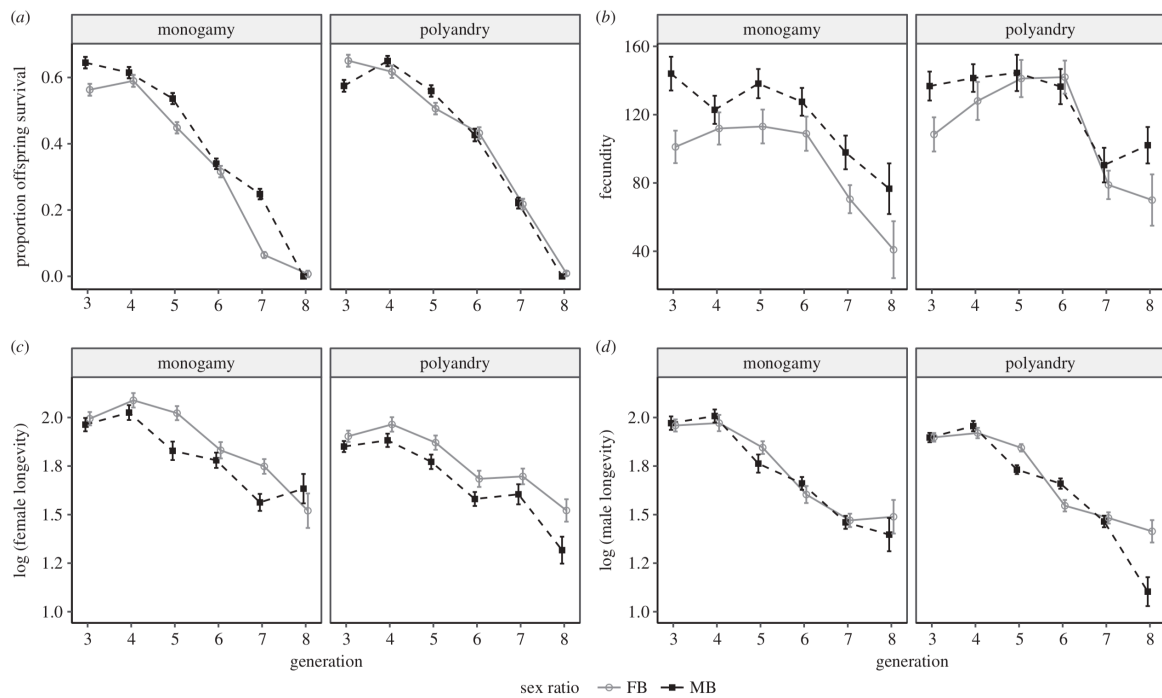
Figures

Figure 1. Comparisons of the effect of sexual selection (MB or FB) and mating system (monogamy or polyandry) treatments on a) proportion offspring survival, b) female lifetime fecundity, c) log transformed female longevity and d) log transformed male longevity from the increasing temperature experiment across F_{3-8}. Weak sexual selection (FB) is indicated by light grey hollow circles and solid lines and strong sexual selection (MB) indicated by dark grey solid squares and dashed lines. Males and females placed within monogamous or polyandrous mating systems during fitness assays are shown in the left and right panels, respectively. Error bars indicated standard error.

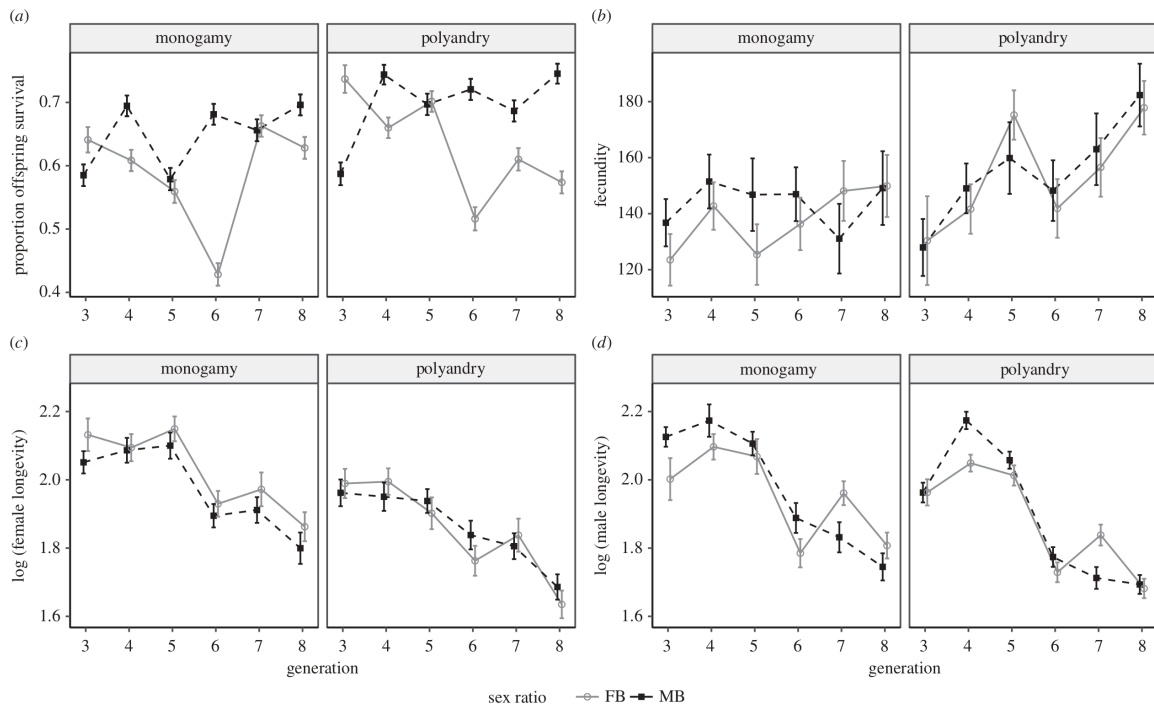**Figure 2.** Comparisons of the effect of sexual selection (MB or FB) and mating system (monogamy or polyandry) treatments on a) proportion offspring survival, b) female lifetime fecundity, c) log transformed female longevity and d) log transformed male longevity from the stable temperature experiment across F_{3-8}. Weak sexual selection (FB) is indicated by light grey hollow circles and solid lines and strong sexual selection (MB) indicated by dark grey solid squares and dashed lines. Males and females placed within monogamous or polyandrous mating systems during fitness assays are shown in the left and right panels, respectively. Error bars indicated standard error.