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The effect of sexual selection on adaptation and extinction under increasing temperatures

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

1. 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 genetic quality of the bearer via the 'genic capture' mechanism [21–24]. In these systems, sexual selection can influence mean population fitness by skewing reproductive success in favour of males with more beneficial alleles and/or fewer deleterious mutations than the overall population average [11–13]. These effects are likely to be especially important during environmental change: Lorch et al. [15] proposed that those individuals most suited to the new environment will have the greatest expression of condition-dependent sexually selected traits, skewing reproductive success in their favour. As a consequence of the increased reproductive success experienced by these 'high-quality' males, sexual selection can increase the proportion of alternative beneficial alleles in a population and enhance adaptation rates to novel and changing environments [15,16]. Recent laboratory work has provided support for these ideas, with populations of seed beetles, Callosobruchus maculatus, reared on a novel diet [25] and flour beetles, Tribolium castaneum, exposed to a pesticide [26] showing reduced adaptation rates when sexual selection was experimentally removed. Additionally, monogamous populations of bulb mites, Rhizoglyphus robini, had decreased fitness and a greater tendency to go extinct compared with polygamous populations when exposed to a raised temperature [27]. Similarly, strong sexual selection has been shown to lead to faster removal of experimentally induced deleterious mutations [28] (but also see [29,30]) and to reduce extinction rates when populations are inbred, as seen in R. robini [31] and T. castaneum [32].

By contrast to these positive effects of sexual selection, field studies have tended to find different patterns, with two studies indicating that increased sexual selection could increase extinction rates [17,33]. This could arise from the high costs of sexually selected traits [10]. Alternatively, because sexual selection reduces the effective population size, genetic drift and increased inbreeding can potentially reduce genetic diversity [14]. Furthermore, recent modelling work suggests that small populations may be at higher risk of extinction when sexual selection is strong due to increased risk of demographic stochasticity [16] providing a possible explanation for the association between increased extinction rates and sexual selection observed in the field [17,33]. Finally, a number of laboratory studies have shown that sexual conflict may retard the adaptive capacity of populations because traits favoured by male reproductive success act antagonistically to female fitness reducing the overall viability of a population [34–37].

All previous experimental work has used step changes in an environmental factor to explore the influence of sexual selection on adaptation rates [25–27,34–36,38]. Many of the most important changes in the environment today, however, are directional, with continuous change happening across

many generations [1,39]. Continuous environmental change imposes a rather different selective environment to that experienced by a population exposed to a step change in its environment. In the latter case, selection will initially be directional but as the population adapts selection will become stabilizing. In the case of continuous environmental change, however, there will be a persistent lag between the phenotypic optimum and the environmental variable, and selection will always be directional in nature. With a step environmental change, alleles which give a selective benefit when environmental change happens will continue to be selected for as the population adapts unless new genetic variants or combinations which give an even closer fit to the new environment arise in the population. With a continuous change, alleles which give a selective benefit when the environment begins to change might lose their selective advantage when further change happens, and population persistence will be more dependent on the rate of creation of new genetic variants and combinations than in the case of a step environmental change [3,40]. Given these differences, whether sexual selection will affect adaptation under directional change in the same way as under a step change is not clear. Martínez-Ruiz & Knell [16] modelled the effect of continuous environmental change and found that sexual selection did lead to enhanced population persistence, possibly even more so than when a step change was modelled, although it should be noted that the purpose of this model was not to compare these environmental scenarios.

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

2. Material and methods

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

In both experiments, a set of fitness assays were performed every generation from F_3 onwards and were carried out at the

temperature currently experienced by the population within their respective experiment. The fitness assays measured total female fecundity and by using a subset of eggs, proportion offspring survival. The longevity of all male and female adult moths used during these assays was also recorded. During fitness assays, an extra treatment was included to investigate phenotypic effects of sexual selection on individual female fitness. In both the stable and increasing temperature experiments, moths from both strong and weak sexual selection treatments (MB and FB, respectively) were randomly assigned to either monogamous (one male: one female) or polyandrous (three males: one female) mating system treatments (electronic supplementary material, see supplementary method and figure S1 for further details).

Statistical analysis was performed using mixed effects models with population as a random effect to account for repeated measures within and between generations. The same analysis was performed for both datasets from the stable and increasing temperature experiments, unless stated otherwise. Direct comparison between the temperature experiments should be made with caution as the statistical analysis was carried out within and not between temperature experiments. Generalized linear mixed effects models with Poisson and binomial error structures were fitted to the fecundity and offspring survival data, respectively. To account for overdispersion in these models an observation level random effect was also included [42,43]. Standard linear mixed effects models were fitted to longevity data, which was log transformed to reduce heteroscedasticity. Owing to extremely low offspring survival in generation F_8 in the increasing temperature experiment, the analysis was performed on F_{3-7} only for these data. Generation was fitted as a factor rather than a continuous explanatory variable because exploratory analysis demonstrated that it was difficult to fit curves which gave a good fit to these data without using rather complex nonlinear models. Because generation was fitted as a factor, temperature was not used as an explanatory variable in the increasing temperature experiment. In all models sexual selection treatment (MB or FB), mating system treatment (monogamy or polyandry) and generation, plus interaction terms up to the third order were used as explanatory variables. To account for pseudoreplication of male longevity from polyandrous mating system treatments, an extra random effect of vial number was included in analyses of male longevity (electronic supplementary material, see supplementary method for further details).

3. Results

(a) Increasing temperature experiment

All populations experiencing an increasing temperature became extinct when the temperature reached $35°C$ at generation F_9. There was no effect of the strength of sexual selection on population persistence in the face of increasing temperatures, indicated by a non-significant interaction between sexual selection treatment and generation ($\chi^2 = 12.27$, d.f. = 1, $p = 0.140$; electronic supplementary material, figure S2, table S1, and supplementary method). The strength of sexual selection did, however, have significant effects on both fecundity and offspring survival before population extinction.

The minimal adequate model fitted to the offspring survival data retained the two-way interaction between sexual selection treatment (MB or FB) and mating system treatment (monogamy or polyandry: $\chi^2 = 6.2$, d.f. = 1, $p = 0.013$; figure 1a; electronic supplementary material, table S2). Additionally, the main effect of generation was also retained

($\chi^2 = 220.25$, d.f. = 1, $p < 0.001$). The latter arises from a clear effect of increasing temperature (as indicated by generation) in reducing offspring survival, with survival rates also depending on both the sexual selection and mating system treatments. When monogamous mating was enforced during the fitness assays, MB (strong sexual selection) populations showed consistently higher offspring survival than FB (weak sexual selection) populations, with survival being on average 8% higher. This effect was especially notable in the first generation after a temperature increase (figure 1a). When polyandrous mating was allowed in the fitness assays this effect was not seen and offspring from both FB and MB lines had survival that was comparable to that of MB offspring in the enforced monogamy treatment. Weak sexual selection thus led to decreased offspring survival, but only when females were not allowed to select their mates.

The minimal adequate model fitted to the fecundity data showed similar effects, retaining both the two-way interactions between sexual selection and mating system treatments ($\chi^2 = 3.88$, d.f. = 1, $p = 0.049$; figure 1b; electronic supplementary material, table S2) and mating system treatment and generation ($\chi^2 = 13.08$, d.f. = 1, $p = 0.023$). Under enforced monogamy MB females consistently had a higher fecundity compared with FB females, laying 32 more eggs each on average. Allowing polyandry during fitness assays tended to increase the fecundity of FB females and the observed difference in MB and FB fecundity when under enforced monogamy largely disappeared. Inspection of figure 1b and model summary indicates that the interaction between mating system treatment and generation is largely driven by polyandrous females having increased fecundity in generation F_8 only, and therefore no overall meaningful pattern can be discerned. Upon further inspection however, fecundity was reduced by increasing temperature (as indicated by generation), but only once temperatures were increased by $6°C$ in generations F_7 and F_8.

Female longevity decreased throughout the experiment, indicated by a main effect of generation ($\chi^2 = 250.49$, d.f. = 1, $p < 0.001$; figure 1c; electronic supplementary material, table S2). Furthermore, female longevity was notably reduced by strong sexual selection, with females from MB populations living for approximately 1 day less than those from FB populations ($\chi^2 = 64.27$, d.f. = 1, $p < 0.001$). The mating system treatment had a similar effect on female longevity: females exposed to a polyandrous mating system also lived for approximately 1 day less than monogamous females ($\chi^2 = 90.55$, d.f. = 1, $p < 0.001$).

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

(b) Stable temperature experiment

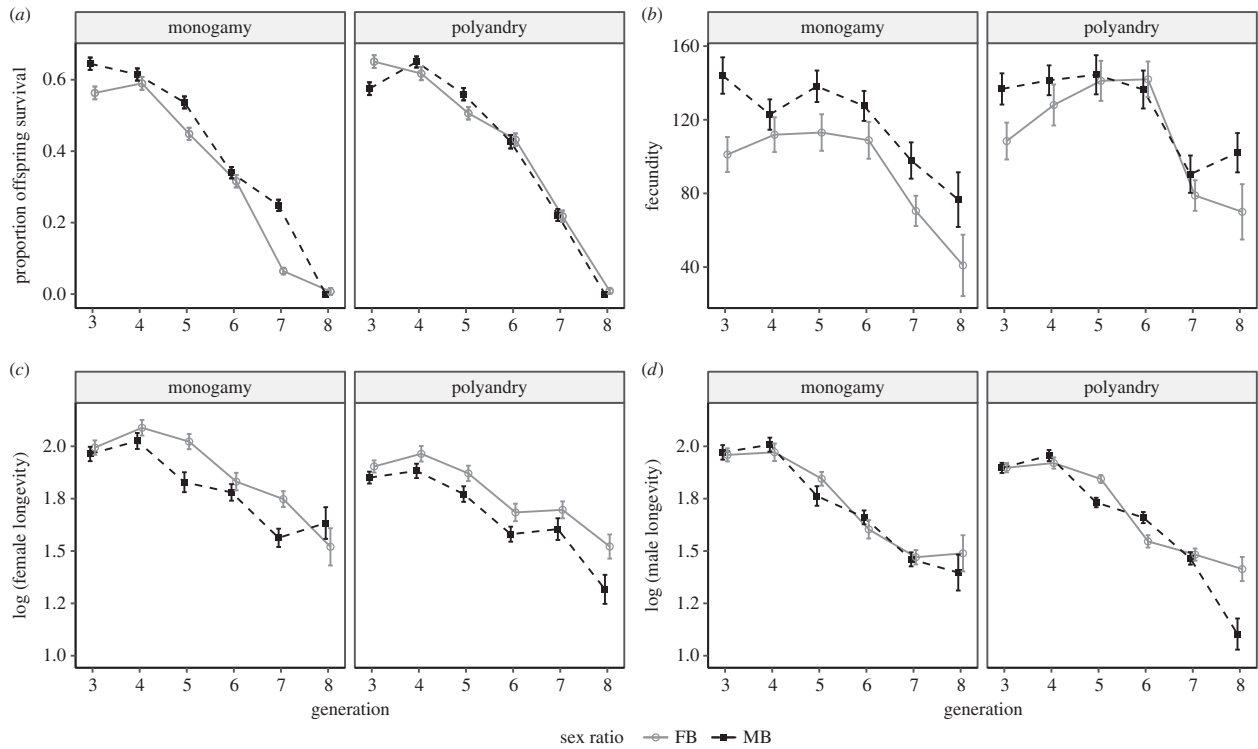When temperatures were stable throughout the experiment, the minimal adequate model fitted to offspring survival

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) is 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 indicate standard error.

data retained a significant two-way interaction between the sexual selection treatment and generation ($\chi^2 = 26.47$, d.f. = 1, $p < 0.001$; figure 2a; electronic supplementary material, table S3). This two-way interaction arises because although there were differences in the survival of MB and FB offspring between generations, these differences were not consistent across the entire experiment. By contrast, having the opportunity for mate choice and multiple mating within the polyandrous mating system treatment tended to increase offspring survival ($\chi^2 = 5.91$, d.f. = 1, $p = 0.015$). Across the entire experiment, polyandrous females had, on average, a 7% higher offspring survival compared with females forced to mate monogamously.

Fecundity was influenced by the mating system treatment, with polyandrous females having increased fecundity in a number of generations ($F_{5, 7, 8}$), indicated by a two-way interaction between mating system treatment and generation ($\chi^2 = 14.75$, d.f. = 1, $p = 0.012$; figure 2b; electronic supplementary material, table S3). There was no effect of sexual selection treatment on female fecundity ($\chi^2 = 0.01$, d.f. = 1, $p = 0.952$).

Female longevity decreased during the last three generations of the experiment ($\chi^2 = 161.58$, d.f. = 1, $p < 0.001$; figure 2c; electronic supplementary material, table S3). There was a significant main effect of mating system treatment, females from polyandrous mating systems tended to live for approximately 1 day less than monogamous females ($\chi^2 = 69.56$, d.f. = 1, $p < 0.001$). There was no effect of sexual selection treatment on female longevity ($\chi^2 = 0.36$, d.f. = 1, $p = 0.546$).

There was also a general trend for male longevity to decrease in the latter half of the experiment. The significant two-way interaction between generation and sexual selection

treatment was retained in the minimal adequate model ($\chi^2 = 21.43$, d.f. = 1, $p < 0.001$; figure 2d; electronic supplementary material, table S3) and largely driven by differences within generations, meaning general patterns are difficult to discern. Male longevity was also reduced by the polyandrous mating system in comparison to the longevity of males under enforced monogamy ($\chi^2 = 21.68$, d.f. = 1, $p < 0.001$).

4. Discussion

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

The results from females assayed with enforced monogamy suggest that sexual selection is acting to enhance the promotion of beneficial alleles within a population and facilitate adaptation to increasing temperatures through 'good
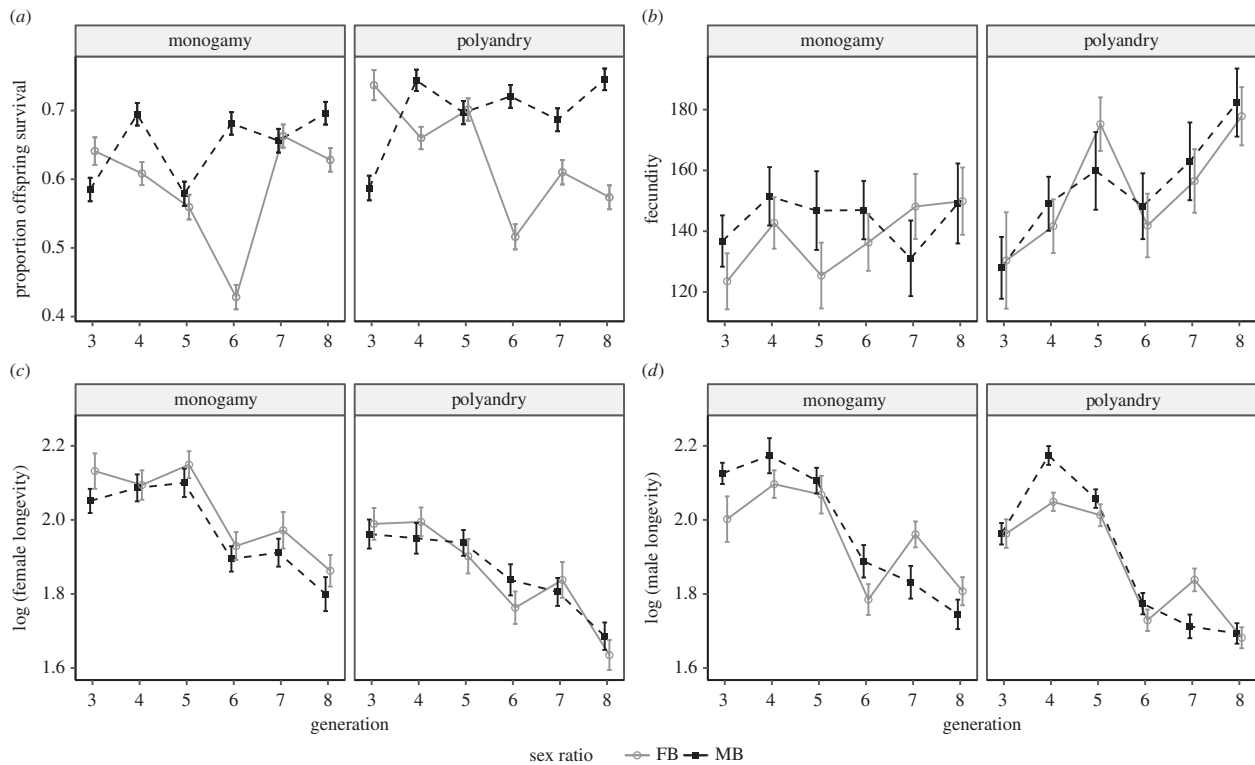
Figure 2. Comparisons of the effect of sexual selection (MB or FB) and mating system (monogamy or polyandry) treatments on (*a*) proportion offspring survival, (*b*) female lifetime fecundity, (*c*) log transformed female longevity, and (*d*) log transformed male longevity from the stable temperature experiment across F_{3-8}. Weak sexual selection (FB) is indicated by light grey hollow circles and solid lines; and strong sexual selection (MB) is 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 indicate standard error.

genes' mechanisms of sexual selection. This indicates that when the environment changes continuously, sexual selection can provide similar benefits to those found by previous empirical studies which examined the effect of sexual selection on adaptation when the environment undergoes a step change [25–27]. In this case, however, the improved fitness associated with strong sexual selection was not sufficient to delay extinction as temperatures continuously increased.

We did not directly assess the strength of condition-dependence of sexually selected traits, but we did find that males placed in a polyandrous mating system during fitness assays experienced reduced longevity compared with those in monogamous conditions. Sexual selection is known to be costly to males and has been shown experimentally to reduce male longevity in a number of taxa (e.g. [44–46]); these costs are likely to increase with the presence of rivals [47,48] and possibly explain the observed reductions in male longevity. Costly traits are expected to be condition-dependent [21] and the genic capture model offers a probable mechanism to explain the observed increase in offspring survival and female fecundity in those populations exposed to increasing temperatures.

By contrast with the increasing temperature experiment, there was no consistent effect of strong sexual selection in the stable temperature experiment. This could be because the benefits of sexual selection are small and hard to detect in populations close to their adaptive peaks, or alternatively, any benefits of sexual selection could be outweighed by the cost imposed through sexual conflict, a similar finding to a number of previous experiments [25,49]. This latter explanation is possible because intra-locus sexual conflict within *P. interpunctella* is known to occur [41].

The difference between the assays conducted on females experiencing enforced monogamy and those in a polyandrous mating system is striking, particularly in those populations evolving with weak sexual selection. The increased offspring survival associated with polyandry is potentially due to females being able to choose to mate with males of 'higher' quality. The increased fecundity in polyandrous females appears to be related to changes in reproductive allocation [50]. Across both experiments, polyandrous females tended to have an increased egg laying rate over the first 96 h of their lives (electronic supplementary material, figures S3 and S4, tables S2 and S3, and supplementary method) which appears to be at the expense of longevity. *P. interpunctella* adults do not feed and it appears that they are following a 'live fast, die young' strategy: when allowed to choose a mate they appear to be investing more resources in reproduction than when monogamy is enforced, leading to higher reproductive output concentrated in a shorter life. Alternatively, polyandry might provide insemination advantages by increasing the genetic compatibility of gametes [51], or polyandrous females might be able to derive some form of nutritional benefit from the ejaculate of multiple males [52].

In the increasing temperature experiment, there was no apparent fitness benefit from polyandry in the strong sexual selection lines. It is possible that this is because selection led to all the males in these lines having higher fitness because 'low-quality' males would have reduced reproductive success in these lines by comparison with the weak sexual selection lines. Alternatively, it is possible that the males in these lines were also being selected for greater competitive ability, reducing the likelihood of a female mating with the 'best' male from a group: if selection in these lines

enabled males to acquire matings via harassment or similar means then this might negate the benefits arising from polyandry. These results highlight a potentially important effect which has largely been overlooked by previous experimental designs: evolved and phenotypic effects of both sexual selection and sexual conflict are likely to be acting and dependent on each other, and it is only because we manipulated sexual selection at both the population and individual level that this came to light. Had we only used a monandrous mating system in the fitness assays then the picture would have been much simpler, but we would not have uncovered this more subtle and complex set of effects.

As population sizes are reduced by increasing temperatures there will be a corresponding reduction in population genetic diversity and increased inbreeding, potentially causing populations to enter an extinction vortex [53]. In contrast to Plesnar-Bielak et al. [27], the positive evolutionary effects of strong sexual selection in the present study were unable to delay this process and the persistent increases in temperature drove all populations to extinction at a similar rate. This indicates that the rate of temperature increase was greater than the critical rate of environmental change [4] and that even with strong sexual selection, adaptation was not swift enough to enhance survival. Worryingly, the rate of increase of temperature in this experiment is comparable to those which longer-lived species with slow generation times are predicted to experience under climate change [1].

If the temperature increases were halted at approximately 31°C or if the rate of temperature increase was reduced, strong sexual selection might have delayed the extinction of MB populations, for two reasons. Firstly, we observed evolutionary effects of strong sexual selection increasing both female fecundity and offspring viability at increasing temperatures, suggesting that adaptation was indeed occurring faster within MB populations; and secondly, there are direct and indirect benefits of polyandry within the increasing temperature experiment. Given that females from MB populations are generally polyandrous,

whereas females from FB populations are likely to only mate once [54], the observed benefits of polyandry would on average be more pronounced in populations under strong sexual selection. Understanding how variation in sexual fitness is affected by differing rates and degrees of environmental change remain important areas for future studies to address [6].

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

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