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RESEARCH PAPER

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Sexual and ecological selection on a sexual conflict gene

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Abstract

Sexual selection and conflict can act on genes with important metabolic functions, potentially shaping standing genetic variance in such genes and thus evolutionary potential of populations. Here, using experimental evolution, we show how reproductive competition intensity and thermal environment affect selection on phosphogluconate dehydrogenase (*6Pgdh*)—a metabolic gene involved in sexual selection and conflict in the bulb mite. The S allele of *6Pgdh* increases male success in reproductive competition, but is detrimental to S-bearing males' partners. We found that the rate of the S allele spread increased with the proportion of males in the experimental populations, illustrating that harm to females is more easily compensated for males under more intense sexual competition. Furthermore, we found that under equal sex ratio, the S allele spreads faster at higher temperature. While the direction of selection on *6Pgdh* was not reversed in any of the conditions we tested, which would be required for environmental heterogeneity to maintain polymorphism at this locus, our study highlights that ecological and sexual selection can jointly affect selection on important metabolic enzymes.

KEYWORDS

balancing selection, environment-driven selection, genetic polymorphism, genetic variation maintenance, genotype-by-environment interaction for fitness, interlocus sexual conflict

1 | INTRODUCTION

Sexual conflict is often associated with arms race dynamics, which can lead to enhancement of traits involved in the conflict or their replacement with new traits that are more effective in securing reproductive interests of their bearers (Brockhurst et al., 2014; Rowe, Chenoweth, & Agrawal, 2018). Such dynamics result in a series of selective sweeps at one or more loci (Rowe et al., 2018) or generate positive selection in a group of molecules of similar function (Swanson, Clark, Waldrip-Dail, Wolfner, & Aquadro, 2001). In theory, however, sexual conflict could also promote polymorphism at the underlying genes (Brockhurst et al., 2014; Rowe et al., 2018). Such polymorphism could increase the potential of a population to respond to environmental change, which often initially relies on standing genetic variation (Barrett & Schluter, 2008). Yet, processes driving polymorphism in genes involved in sexual conflict received far less attention compared to those leading to escalatory arms race.

One mechanism potentially maintaining polymorphism in genes involved in sexual conflict is negative frequency-dependent selection, resulting from Red-Queen dynamics analogous to antagonistic coevolution between hosts and parasites (Brockhurst et al., 2014; Rowe et al., 2018). Another potential mechanism involves negative pleiotropy (Zajitschek & Connallon, 2018), where a trait beneficial to male competitiveness is associated with detrimental pleiotropic effects on other fitness components. For example, in the soay sheep, a gene causing expression of enlarged horns, a trait beneficial to male reproductive success, has a negative pleiotropic effect on survival (Johnston et al., 2013). However, this sexually selected trait does not seem to be involved in sexual conflict.

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Genotype-by-environment interactions for fitness in heterogeneous environments constitute yet another mechanism with considerable potential to maintain polymorphism in sexual conflict-related genes. For example, an allele bearing advantage in male–male competition might be favourable in benign, for example less energetically demanding environments, but its expression may be too costly in harsh conditions, in which an alternative allele would be selected for. As environmental variability is a rule rather than an exception, such environment-dependent selection might be a potent force maintaining genetic variation (Gillespie & Turelli, 1989; Hedrick, 1986; Kokko & Heubel, 2008; Via & Lande, 1987). However, while a number of studies have shown genotype-by-environment interactions for fitness in sexually selected traits (e.g. Qvarnström, 1999; Welch, 2003; Plesnar-Bielak, Skwierzyńska, Hlebowicz, & Radwan, 2018; see Ingleby, Hunt, & Hosken, 2010 for review), less effort has been devoted into investigating maintenance of polymorphism in genes involved in sexual selection and conflict (Rostant, Kay, Wedell, & Hosken, 2015).

Here, we explore environmental factors which may potentially shape selection patterns on and maintain polymorphism of the phosphogluconate dehydrogenase (*6Pgdh*)—a metabolic gene under strong sexual selection and subject of sexual conflict in the bulb mite, *Rhizoglyphus robini* (Acari, Acaride) (Konior, Radwan, Kołodziejczyk, & Keller, 2005; Skwierzyńska & Plesnar-Bielak, 2018). 6Pgdh is an enzyme in pentose phosphate cycle, which is an alternative to glycolysis for converting glucose and generates NADPH used in fatty acids synthesis and other reduction transformations (Murray, Granner, Mayes, & Rodwell, 2003). The pentose phosphate pathway is also a source of ribulose-5-phosphate used in the biosynthesis of nucleotides (Murray et al., 2003). In the bulb mite, polymorphism in *6Pgdh* is associated with large differences in male fitness (Konior et al., 2005; Skwierzyńska & Plesnar-Bielak, 2018). Males homozygous for the "winning" S allele produce more sperm, mate more frequently and consequently win reproductive competition with males homozygous for the "losing" F allele (with SF heterozygous males showing trait values intermediate between both homozygotes (Łukasik, Zygadło, & Radwan, 2010; Skwierzyńska & Plesnar-Bielak, 2018)). While female *6Pgdh* genotype has no direct effect on fecundity, mating with SS males decreases female fitness compared to mating with FF males (Konior et al., 2005; Łukasik et al., 2010; Skwierzyńska & Plesnar-Bielak, 2018). Thus, *6Pdgh* is a rare example of a polymorphic gene that has been demonstrated to be involved in sexual conflict.

One potential factor affecting selection on *6Pdgh* is social environment. Under intense reproductive competition between males, the S allele is selected for (Konior et al., 2005). On the other hand, Konior et al. (2005) speculated that when sexual selection is weak, which may occur at low densities and particularly when populations are female-biased, costs paid by harming males in terms of reduced reproductive output of their partners cannot be compensated by obtaining more partners. Consequently, harming males may ultimately have fever progeny, which would favour the F allele bearers. In the bulb mites, female bias may often occur due to male mortality associated with aggression of armoured fighter males, which coexist with unarmoured, benign scrambler males in many populations (Radwan, 1995; Radwan & Klimas, 2001). At low population densities, a single fighter can sometimes even monopolize local groups of females by killing all his rivals (Radwan & Klimas, 2001), in which case reproductive success of the harem owner would be closely linked with female fitness. Thus, when sexual selection is weakened due to female-biased sex ratio, a male might hardly benefit from bearing an allele increasing his competitiveness at the expense of his female partner.

Another factor that might reverse selection on *6Pgdh* alleles is ambient temperature. Thermal conditions affect nearly all aspects of ectotherm life history, driving metabolism intensity and metabolic costs of body structures and behaviours (reviewed in Angilletta, 2009). *6Pgdh*, along with other enzymes associated with glycolytic pathway, is subjected to selection resulting in clinal or seasonal variation in temperature in *Drosophila melanogaster* (reviewed in Eanes, 2011). It is thus plausible that thermal conditions could shape the patterns of *6Pgdh* allele frequencies in the bulb mites. This is consistent with the fact that in laboratory conditions, where populations are maintained at 24°C, a temperature much higher than that experienced by mites in nature for most of the year, the S allele rapidly goes into fixation (Konior et al., 2005). However, both alleles appear to persist in natural populations (Konior et al., 2005; Łukasik et al., 2010). The frequency of the F allele changes between years and has been reported to range from 0.34 to below 0.05 in the same population over a two-year period (Łukasik et al., 2010). The maintenance of both alleles and their changing frequencies suggest that the persistence of polymorphism might be associated with variation in thermal conditions.

We use an experimental evolution approach to investigate how the intensity of reproductive competition (manipulated by sex ratio) and temperature affect selection on *6Pgdh* frequencies in bulb mite populations. We trace changes in *6Pgdh* frequencies in replicate populations for 10 generations under three male proportions (0.3, 0.5, 0.7) and temperatures (18, 20, 24°C). Furthermore, we test the capacity of temperature and/or sex ratio variation to maintain *6Pgdh* polymorphism. Such capacity would be corroborated by a cross-over genotype-by-environment interaction for fitness of the S and the F allele bearers. Thus, we predict that the "winning" S allele would be selected for in male-biased populations and/or at 24°C, but the F allele should increase in frequency in female-biased populations and/or at 18°C.

2 | MATERIALS AND METHODS

2.1 | 6Pgdh genotyping

To genotype individuals, polymorphic *6Pgdh* fragments were amplified using PCR. We used three PCR primers that allow to differentiate individuals possessing the F allele (SF and FF) from those lacking it (SS) (Skwierzyńska & Plesnar-Bielak, 2018). The genotype of the individual of interest was assessed from genotypes of its offspring

produced with a partner of SS genotype coming from the laboratory population in which the S allele had been fixed. Thus, for an SF heterozygote we expected 50% SS homozygotes among its offspring and no SS homozygotes among FF homozygotes' offspring.

2.2 | Establishment of source population

To establish experimental evolution populations, we used the source population enriched for the F allele as described by Skwierzyńska and Plesnar-Bielak (2018). In brief, we first collected ca. 100 individuals from a natural population polymorphic at *6Pgdh* and allowed them to reproduce freely in standard laboratory conditions (24°C, >90% humidity, constant darkness, powdered yeast provided ad libitum as a food source) for one month (ca. two generations). Then, to ensure that the F allele was maintained in our source population at an appreciable frequency before starting the experimental evolution, we used the following procedure: (a) we randomly created 100 pairs of individuals and allowed them to reproduce in individual vials with no competition from other males (this was done because the F allele is rapidly removed from laboratory populations by selection due to higher reproductive success of S-bearing males); (b) after 7 days of interaction, all parents were checked for the presence of the F allele. At least one parent was the bearer of the F allele in 36 pairs, whose offspring was used to establish the source population with an elevated proportion of the F allele (0.26); (c) we allowed such a population to expand freely for an additional month to obtain a sufficient number of individuals for the experimental evolution.

2.3 | Experimental evolution under different sex ratios

We established 15 experimental populations differing in sex ratio (five replicates in each of the three sex ratio treatments). The proportions of males were 0.3, 0.5 and 0.7.

Each generation, 100 virgin individuals (with sex proportion matching sex ratio treatments) were transferred to 2-cm-diameter plastic containers and allowed to interact for 5 days. Afterwards, the parents were removed and the eggs were left to develop. As the number of females differed between treatments, densities of developing juveniles could also differ, with the highest densities in female-biased populations. However, an excess of food provided and, the size of containers preventing overcrowding, minimized competition between developing mites. Therefore, variation in juvenile densities should not have contributed to selection differences between treatments. About 10–12 days after removal of adults, when most of the nymphs achieved the last juvenile stage (trithonymph), we isolated them into individual vials to obtain virgin individuals for the next generation. After they reached maturity, we transferred appropriate numbers of males and females to a common container to start the next generation. After generations 1, 5 and 10, a random sample of ca. 30 individuals was genotyped for *6Pgdh*.

2.4 | Experimental evolution under different temperatures

We established 15 experimental populations evolving at 24, 20 or 18°C (five replicates in each treatment). In each population, every generation, 50 virgin males and 50 virgin females were placed at an experimental temperature. Each new generation was established as described above for sex ratio manipulated populations. After generations 1, 5 and 10, a random sample of ca. 30 individuals was genotyped for *6Pgdh*. Allele frequencies at the corresponding generations were assessed at different time points for different temperatures, as temperature strongly affects development time, with mites reaching adulthood after 16–21 days at 18°C and 10–15 days at 24°C (Plesnar-Bielak et al., 2018).

2.5 | Statistical analysis

First, for each of the two experiments we used repeated measure ANOVA to see how allele frequencies change over the course of evolution. Proportion of the S allele, arcsine transformed for normality, was a response variable, with treatment (either sex ratio or temperature) as a factor repeated over generations. Normality of residuals was checked by visually inspecting Q-Q plots. As for both experiments we found significant treatment by generation interactions (see Section 3), we made follow-up analyses for each tested generation separately to see when allele frequencies started to differ between treatments. This time we used generalized linear model with quasibinomial distribution to account for underdispersion in our data. A vector with the S and the F counts for each population was a response variable, and treatment (sex ratio or temperature) was a fixed factor. The analyses were done in R 3.5.1 (R Core Team, 2018). Glm function from "stats" was used to construct generalized linear models, and lmer function (Bates, Mächler, Bolker, & Walker, 2015) from "lme4" package was used to build general linear mixed effects models.

3 | RESULTS

3.1 | Experimental evolution under different sex ratios

Analysing the S allele proportions using repeated measure ANOVA, we found a generation by treatment interaction ($F_{2,12} = 53.19$, $p < .001$, Figure 1) indicating that allele trajectories (changes in allele frequencies over generations) differed between populations with different sex ratios. The main effects of generation ($F_{1,12} = 527.66$, $p < .001$) and treatment ($F_{2,12} = 146.6$, $p < .001$) were also significant, with the S proportion increasing over time and being overall higher in more male-biased populations. Average selection coefficients estimated from first five generations (see Supplementary Material for methods) ranged between 0.18 for female-biased

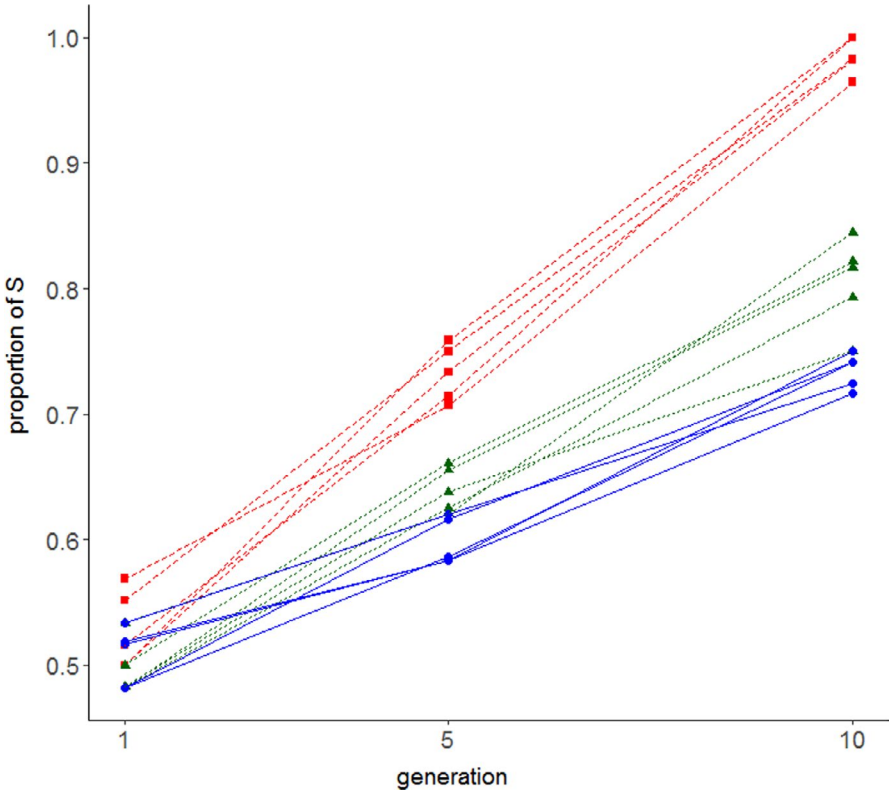

FIGURE 1 Proportions of the S allele in male-biased (male proportion 0.7, red squares, red dashed lines), unbiased (male proportion 0.5, green triangles, green dotted lines) and female-biased (male proportion 0.3, blue circles, blue solid line) experimental populations at generations 1, 5 and 10 of experimental evolution

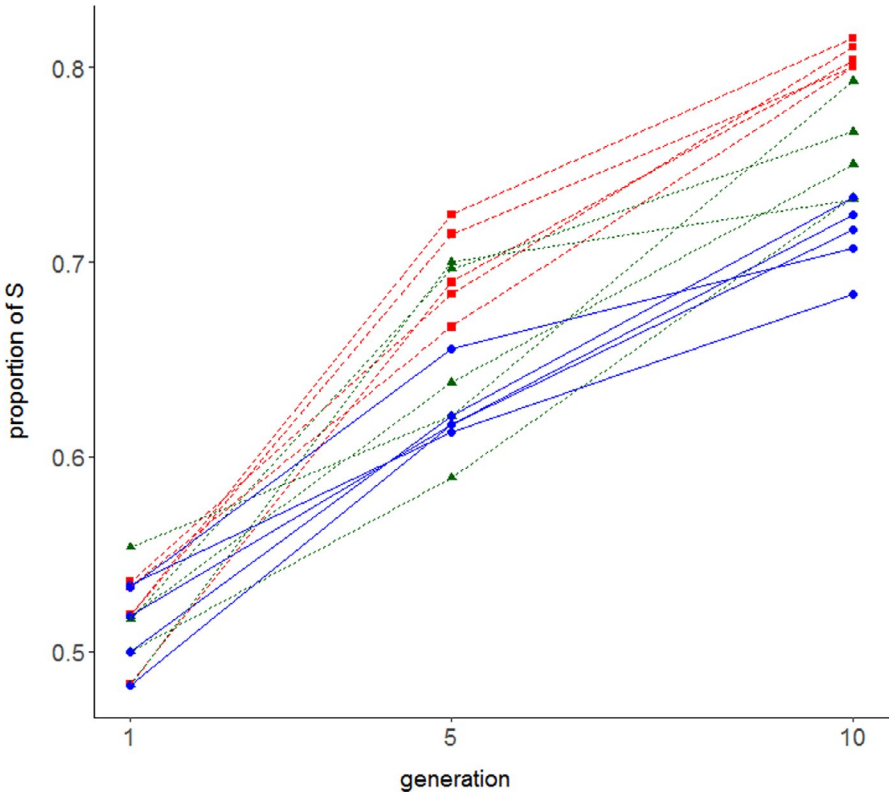

FIGURE 2 Proportions of the S allele in populations evolving at 24°C (red squares, red dashed lines), 20°C (green triangles, green dotted lines) and 18°C (bleu circles, blue solid line) experimental populations at generations 1, 5 and 10 of experimental evolution

treatment to 0.37 for male-biased treatment (Supplementary Material). Furthermore, selection coefficients apparently increased between generation 5 and 10, particularly in male-biased treatment (Supplementary Material). Separate analyses of allele proportions for the generations showed that the S allele proportions did not differ between treatments at the start of experimental evolution (generation 1: $F_{1,12} = 1.82$ $p = .205$), but differentiated in generation 5 ($F_{1,12} = 60.13$, $p < .001$) and generation 10 ($F_{1,12} = 97.27$, $p < .001$).

3.2 | Experimental evolution under different temperatures

The S allele trajectories varied between populations evolving at different temperatures (generation by temperature interaction: $F_{2,12} = 18.34$, $p < .001$, Figure 2). At each temperature, however, the S proportion increased over generations ($F_{1,13} = 1{,}342.61$, $p < .001$). The effect of temperature treatment was also significant ($F_{2,13} = 20.95$, $p < .001$), with higher S proportions at higher temperature and estimated selection coefficients averaged for first five generations ranging between 0.2 at 18°C to 0.32 at 24°C (Supplementary Material). Further analyses revealed that the S proportion did not differ between temperatures at generation 1 ($F_{1,12} = 0.42$ $p = .96$), but diverged at generation 5 ($F_{1,12} = 6.27$ $p = .014$) and generation 10 ($F_{1,12} = 31.63$, $p < .001$).

4 | DISCUSSION

Polymorphisms in genes associated with sexual conflict may facilitate populations' adaptation to environmental change, yet our understanding of the processes maintaining these polymorphisms and how they are shaped by ecological factors is extremely limited. In the current study, we demonstrate that selection driving phosphogluconate dehydrogenase (*6Pgdh*) frequencies is environment-dependent. Firstly, we show that the strength of selection on this locus varies with sex ratio, with steeper S frequency increase in male-biased populations with more intense sexual selection and flatter in female-biased ones. Secondly, we demonstrate that selective advantage of the S allele decreases with decreasing temperature.

Selection coefficients favouring the S allele were estimated from 0.18 to 0.2 for female-biased sex ratio and lowest temperature treatments to 0.33 to 0.35 for the highest temperature and male-biased treatment. These values are in line with correspondingly large differences between *6Pgdh* genotypes in copulation rates, sperm production (Skwierzyńska & Plesnar-Bielak, 2018) and competitive fertilization success (Konior et al., 2005). The trajectories of the S allele frequency change were linear, rather than decelerating with generations as expected under constant selection coefficient (see Hartl & Clark, 1997), suggesting positive frequency-dependent selection, particularly at male-biased sex ratio. This result, however, should be treated with caution as positive frequency dependence was supported only in male-biased and female-biased populations, and our analyses turned out to be extremely sensitive to apparently random fluctuations of allele frequencies at generation 5 (see Supplementary Material for in-depth discussion).

For neither ecological factor have we detected a cross-over genotype-by-environment interaction for fitness in *6Pgdh*, as indicated by the S allele increase in all experimental populations. Such a cross-over interaction, with ranks of genotypes reversed by environment, is needed for environmental heterogeneity to maintain genetic variation (Gillespie & Turelli, 1989; Hedrick, 1986; Kokko & Heubel, 2008; Via & Lande, 1987). On the other hand, it is possible that further lowering temperature and/or increasing female sex bias of populations would lead to the reversal of *6Pgdh* genotypes ranking for fitness. Specifically, the temperatures experienced by natural bulb mite populations during some periods of the year might be much lower than the lowest temperature used in our experiment. The bulb mites live on underground parts of plants and average soil temperatures in Poland at the depth of 5 cm range from 1.0 to 1.5°C in winter and from 5.2°C to 18.6°C in spring with a year average of 11.7°C (Ciaranek, 2013). It is possible that in cold seasons, the F allele might temporarily have selective advantage over the S allele, causing a cross-over in reaction norms. Such temporal variation in selection direction could contribute to the maintenance of *6Pgdh* polymorphism observed in natural populations. While using multigenerational experiments at such low temperatures would be difficult due to prolonged generation time of the mites, fitness of the two genotypes could be assessed by direct comparisons.

It is also possible that the maintenance of the F allele in natural populations is facilitated by an interplay between sexual selection intensity and temperature. Specifically, the differences between temperatures in the rate of the S frequency increase suggest that the advantage in sperm competition for the S-bearing males is partly offset by a cost they pay at lower temperatures. Thus, the direction of selection on *6Pgdh* locus at low temperature could depend on the magnitude of benefit gained by the S-bearing males due to sperm competitiveness, hence on sexual selection intensity. In most natural populations, sexual selection might in fact be much weaker than in laboratory conditions due to lower densities. In such populations, where the risk of sperm competition is low, the advantage provided by the S allele is only moderate and may not compensate for the S allele cost associated with thermal conditions. Testing whether this is the case would require an experimental design where sexual selection intensity would be crossed with temperature.

Fitness of *6Pgdh* variants has been shown to be associated with environmental conditions in other species. We found temperature-dependent selection on *6Pgdh* consistent with latitudinal clines of *6Pgdh* allele frequencies observed in *Drosophila melanogaster* (Begun & Aquadro, 1994; Oakeshott, Chambers, Gibson, Eanes, & Willcocks, 1983) and believed to be associated with climatic conditions (Oakeshott et al., 1983). On the other hand, the frequency of *6Pgdh* alleles in the white sands pupfish *(Cyprinodon tularosa)* has been shown to be related to salinity, but not temperature (Stockwell & Mulvey, 1998), showing that the influence of thermal conditions on fitness of bearers of different *6Pgdh* alleles is not universal. Similarly, latitudinal clines of *6Pgdh* frequencies are associated with salinity in mummichog (*Fundulus heteroclitus*) (Powers et al., 1986). In general, while *6Pgdh* variation seems to be maintained by selection in a variety of taxa including plants (Conte, Nodari, Vencovsky, & dos Reis, 2003; Rainey, Mitton, & Monson, 1987), invertebrates (Begun & Aquadro, 1994; Oakeshott et al., 1983) and vertebrates (Powers et al., 1986; Stockwell & Mulvey, 1998), the exact selection factors driving differences between fitness of the two alleles may differ between taxons. While thermal conditions may play a role in some species, the bulb mite is

so far the only example in which *6Pgdh* variants have been shown to influence sexual selection and conflict (Konior et al., 2005; Łukasik et al., 2010; Skwierzyńska & Plesnar-Bielak, 2018) and in which the amount of sexual selection experienced by a population has been shown to influence the intensity of selection on *6Pgdh* (this study).

Overall, our study highlights that sexual selection can interact with ecological factors in affecting selection on metabolic genes crucial for adaptation to environmental conditions. While such genes are widely reported to be under strong selection pressures, selection mechanism remain obscure (Marden, 2013). Our results thus signify that sexual selection and conflict can have important impact on the standing genetic variance in these genes, thus determining the scope for adaptive response to environmental change. However, because we showed that temperature and population sex ratio modulate, but do not reverse, selection on *6Pgdh* variants within the ranges we investigated, further work is necessary to determine how polymorphism of this gene is maintained under natural conditions.

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DATA AVAILABILITY STATEMENT

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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