Review

Is sexual selection beneficial during adaptation to environmental change?

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The role of sexual selection in adaptation is disputed. A balance between sexual and viability selection can be achieved in stable environments, but environmental perturbations could change the costs and benefits arising from sexual selection and influence the rate of adaptation. Here we synthesise theoretical and empirical work on the role of sexual selection in adaptation to changed conditions. Contrasting results have been gained, but the majority of studies suggest that sexual selection has no significant effect or a negative effect on the rate of adaptation. However, once sexually selected traits start to evolve, sexual selection can accelerate adaptation. The role of sexual selection in extinction appears to be minor, but the results could be skewed.

Introduction

Organisms adapt to new conditions through natural selection, whereby individuals best able to cope with the new conditions survive and reproduce. Sexual selection is a part of natural selection that drives the evolution of traits that increase success in the competition for mates and fertilisations [1]. The competition for mates is, however, often costly, and sexual selection can hence favour traits that impose substantial fitness costs at the individual level. Because these costs could influence population viability, it is disputed whether sexual selection is beneficial and accelerates adaptation when populations confront new or changed conditions [2,3].

The question of the role of sexual selection in adaptation has recently gained increased attention, and the first empirical studies are emerging. Here we discuss how sexual selection can modulate the response of populations to environmental change. We start by emphasising the environmental dependence of the costs and benefits of competition for mates and, hence, the environmental dependence of the strength and target of sexual selection. We then proceed to discuss how changes in these factors can influence adaptation to new or changed conditions. The world is presently changing at an accelerating rate, owing to human activities, and the determination of the response of populations to altered conditions is consequently increasing in importance. To be able to predict the future of populations and ecosystems subjected to environmental change and to manage endangered species, we need to clarify the effects of evolutionary forces on populations.

Environmentally induced changes in the costs and benefits of sexually selected traits

At the individual level

Alterations of the environment can change the costs and benefits of sexually selected traits at the individual level, which could have further consequences at the population level and for adaptation to new conditions. Sexually selected traits evolve through sexual selection, that is, through the competition between individuals of the same sex for mates and fertilisations [1]. They are hence beneficial to the individual if they increase the number or quality of offspring produced. However, sexually selected traits are often costly, such as bright colours and conspicuous displays that increase predation risk. Sexually selected traits can therefore impose fitness costs on the individual [4] (Box 1).

Obviously, the costs and benefits of sexually selected traits depend on prevailing conditions [5]. In the African lion *Panthera leo*, for instance, dark-maned males have higher mating success, but the dark colour also increases surface temperatures and results in abnormal sperm and lower food intake [6]. The present increase in temperature due to global warming is therefore predicted to increase the cost of dark manes [6]. Changes in the environment can similarly reduce the benefit of a preference for a trait, if it disrupts the link between signal value and individual quality. For example, reduced visibility due to eutrophication in the breeding areas of the threespine stickleback *Gasterosteus aculeatus* relaxes male–male competition and the social control of male sexual displays. This allows cheating in the advertisement of male competitive and parental ability, which can have detrimental effects on female fitness by reducing offspring survival and possible genetic quality [7,8].

The costs and benefits of sexually selected traits could also change indirectly during environmental change, if individuals adjust the costs and benefits of sexually selected traits to the new conditions through phenotypic plasticity. One possibility is that the amount of time and resources that is invested in the expression and the evaluation of sexual traits is altered depending on environmental conditions. For example, the reduction in visibility in eutrophied waters forces threespine stickleback males to increase the time and effort they spend on sexual displays to attract females, whereas females increase the time they spend on mate evaluation, owing to impaired possibility of evaluating mates [9,10]. These increases in the investment in sexual traits can result in fewer resources being

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Box 1. The costs and benefits of sexually selected traits

Sexually selected traits evolve through direct or indirect selection. Direct selection arises when the choosing sex gains direct benefits, such as more parental care or increased fertility through their mate preferences (or resistance to unwanted mates) [66]. Indirect selection arises when the performance of the offspring is improved through the inheritance of favourable alleles that increase their attractiveness (the Fisherian runaway selection) or viability (the viability indicator, or good genes model) [67].

If sexually selected traits reflect genetic quality, then the viability of the population could increase [2]. Genetic quality has two components: good genes that refer to additive genetic variation in fitness, and compatible genes that refer to nonadditive genetic variation [68]. Whereas good genes increase the general viability of the population, compatible genes require assortative mating for positive effects on population viability because their effect depends on how well the genes of the parents function together in their offspring [69]. Sexual traits that reflect good genes or compatible genes would thus have positive effects on population viability.

Sexual selection can also result in a reduction in individual fitness that could influence population viability, as predicted by the major models of sexual selection. The Fisherian runaway model assumes that the exaggeration of sexually selected traits continues until the benefits in terms of mating success are balanced by the costs of the traits [70,71]. The viability indicator models predict that sexually selected traits become exaggerated in a condition-dependent manner so that the benefit in terms of mating success is balanced by the cost, whereby fitness costs ensure honesty [72]. The sexually antagonistic selection model proposes that manipulative reproductive strategies in one sex harms individuals of the other sex, which results in the evolution of resistance to manipulation and sexually antagonistic coevolution [47,73]. Sexual selection can hence impose both costs and benefits, and whichever dominates at the population level is disputed [16].

available for other fitness traits and can thereby reduce individual fitness under the new conditions.

Phenotypic plasticity and the adjustment of trait expression to new environments could either increase or decrease the adaptive value of sexual traits [11,12]. Plasticity could increase the honesty of sexual signals and the benefit of preferences for the signals if it ensures that the expression of the traits correlates with individual fitness in the new environment. Alternatively, plasticity could result in dishonest signals and maladaptive preferences if it removes the link between quality and trait expression. In particular, genotype-by-environment interaction, where different genotypes show different shifts in trait expression in response to an environmental change, could disrupt the link between trait expression and individual quality [11,12].

Several lines of evidence indicate that phenotypic plasticity and genotype-by-environment interactions in sexual traits are common. For instance, in the waxmoth *Achroia grisella*, the genotype that produces the most attractive ultrasonic signal differs between rearing environments [13]. Similarly, in the collared flycatcher *Ficedula albicollis*, the heritability of a sexually selected trait, the size of the white forehead badge, varies depending on environmental conditions [14]. However, surprisingly little attention has been given to how plasticity influences the costs and benefits of sexually selected traits and their adaptive value under changing conditions [11,15]. In particular, the consequence of plasticity in sexual traits for individual fitness under human-induced, rapid environmental changes is largely unknown.

Changes in the environment could thus alter the costs and benefits of sexual traits at the individual level. This could influence the fitness of the individuals in terms of the number or quality of offspring produced in the new environment.

At the population level

Environmentally induced changes in the number or quality of offspring produced per individual can influence offspring production in the population and thereby affect population dynamics and viability in the new environment (Figure 1). Several theoretical studies have tried to unravel the ultimate effect of sexual selection on population viability. However, different conclusions have been gained, depending on the angle taken [16].

According to the good genes model, mating success is positively correlated with genetic quality and, hence, sexual selection increases the proportion of alleles that are beneficial under the prevailing conditions [4,17]. Sexual selection could then facilitate the fixation of beneficial alleles and the shedding of mutational load, thereby accelerating adaptive evolutionary change and enhancing population viability [2,18]. This assumes that the sexual traits are adaptive, or have evolved to become beneficial, under the new conditions. Looking at the other side of the coin, fitness costs of sexually selected traits at the individual level can reduce the total number or quality of offspring produced at the population level and hence reduce population viability [16] (Box 1). This could retard the adaptation to new conditions.

Empirical studies on the influence of sexual selection on population viability have so far given conflicting results. An early study on *Drosophila melanogaster* found juvenile survival to be augmented when sexual selection was allowed [19], but the results could not be repeated in later experiments [20]. On the contrary, experiments on *D. melanogaster* [21] and on the yellow dung fly *Scathophaga stercoraria* [22] found the removal of sexual selection to enhance reproductive rate, probably the result of a reversal of antagonistic coevolution between the sexes that otherwise can depress female reproduction. Moreover, studies on the bulb mites *Rhizoglyphus robini* found no clear effect of sexual selection on most fitness components [23,24].

Overall, no consensus has been gained on the effect of sexual selection on population viability. Although viability selection often works against sexual selection, equilibrium between the strength of sexual and viability selection is expected to evolve in stable environments [16]. However, changes in conditions could change the relative intensity of the two selection pressures and decrease the viability of the population [16]. The rate of environmental change in relation to the possible rate of adaptation will then determine whether a population persists and flourishes under the new conditions.

Interestingly, studies on human-induced changes in the costs of sexually selected traits suggest that increases in costs can reduce population viability through increased mortality of individuals of high genetic quality. For example, sport hunting of trophy rams of the bighorn sheep *Ovis canadensis* removes the rams with the biggest horns from the population before they reach their reproductive

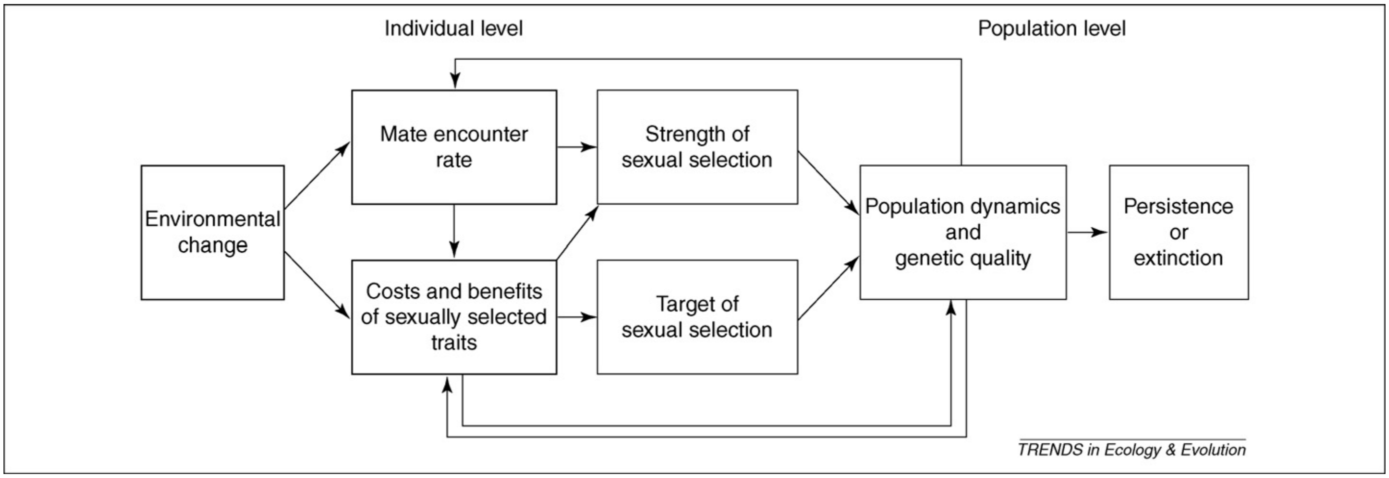

Figure 1. Sexual selection can modulate the response of populations to environmental change. Changes in environmental conditions influence mate encounter rate and the costs and benefits of sexually selected traits, which in turn determine the strength and target of sexual selection. Sexual selection influences the dynamics and viability of the population, which determines whether the population will persist or go extinct. The system is self-regulating in that changes in the dynamics of the population will feed back to the mate encounter rate and the costs and benefits of sexually selected traits and regulate sexual selection.

peak [25]. This has resulted in the evolution of smaller horns and most likely in a reduction in population viability, because the rams with the biggest horns probably are of high genetic quality [25].

There might, however, be mechanisms that can prevent the costs of sexually selected traits from increasing to levels that are detrimental to population survival, irrespective of environmental change. Recently, a link between mating systems and population dynamics has been suggested to prevent detrimental increases in the costs of sexual traits [26]. If the cost of the trait increases, the size of the population will decrease. This will reduce the mate encounter rate and relax the strength of sexual selection, which can favour the evolution of less costly sexual traits. Density dependence in the strength of sexual selection would then make sexual selection self-limiting [26]. The empirical evidence for density dependence in the strength of sexual selection is equivocal. Some studies find the strength of sexual selection to increase with the density of competing individuals, whereas others find it to decrease (reviewed in Ref. [26]). The estimation of the importance of density dependence will therefore have to await further empirical results.

Effects of sexual selection on the rate of adaptation

If the number and quality of offspring produced in the population is altered under the new conditions, as a result of changes in the costs or benefits of sexual traits, then this could influence the rate of adaptation to the new conditions. An increasing number of studies find sexually selected traits to be maladaptive under changed conditions, in that individuals that are not well adapted to the new conditions and are of low quality have a high mating success [7,27–29] (Box 2). This suggests that strong sexual selection could be a burden and slow down the initial adaptation to the changed conditions. Interestingly, empirical studies also show that sexual selection that has been operating in one environment is often relaxed under new conditions, as a result of impaired possibility of mate evaluation or mate choice [9,30,31] (Box 2; Figure 2). This could strengthen the relative importance of selection at other life stages, such as at the juvenile stage. If sexual selection is not adaptive under the changed conditions the relaxation of sexual selection could remove a burden, whereas strengthening of natural selection at other selection stages could accelerate the rate of adaptation.

The rate of adaptation to new conditions depends also on the amount of additive genetic variance (Box 3). If there is no additive genetic variance in the direction of selection,

Box 2. Environmentally induced changes in the strength or target of sexual selection

Changes in the costs and benefits of sexually selected traits could change the strength and target of sexual selection. An increasing number of studies find evidence for the strength of sexual selection being relaxed under changed conditions, usually owing to impaired possibilities of evaluating mates or exerting choice. A classical study on cichlid fishes of the Great Lakes of Africa found that increased turbidity of the water constrained colour vision and interfered with mate choice based on visual cues [65]. This relaxed selection on colouration resulted in a breakdown of reproductive barriers. Similarly, several recent studies on different fish species find that reduced visibility induces more random mating, thereby relaxing the strength of sexual selection on sexual traits [7,9,30,31].

The opposite possibility, that changes in the environment facilitate the evaluation of mates and enhance the strength of sexual selection, has gained less support. In the chuckwalla *Sauromalus obesus*, the density of males and females increases with resource availability, which increases mate encounter rate and results in a stronger female preference for colourful males [74]. Changed environmental conditions can also force individuals to increase their investment in sexual advertisement to gain matings, which could increase the difference among individuals in sexual displays [10]. However, positive effects of enhanced sexual selection on the viability of populations under changed conditions might well be rare, because the probability that random environmental changes would improve mate evaluation or the adaptive value of traits should be low.

If sexual selection on traits that traditionally have been used in mate competition and mate choice is weakened, this could strengthen selection on other traits that are beneficial under new environmental conditions. The target of sexual selection could then change. In support of this, several studies find that different sexual traits are used in different environments [75,76]. For example, the Atlantic mollies *Poecilia mexicana* that inhabit caves use nonvisual cues for mate choice, whereas ancestral surface-dwelling mollies use visual cues [77].

Figure 2. Changes in water turbidity and algae growth can influence the visibility of sexually selected colours and courtship displays in fishes. This can decrease the ability of females to evaluate males, and consequently reduce the strength of sexual selection, as documented in cichlid species of the Great Lakes of Africa [65], the threespine stickleback *Gasterosteus aculeatus* [9] and the sand goby *Pomatoschistus minutus* [30].

then no evolutionary response is expected. Interestingly, a meta-analysis of studies on wild populations suggests that harsh environmental conditions decrease heritability, owing to decreased additive genetic variance, higher environmental variance or genotype-by-environment interactions [32]. The reduced heritability could reduce the ability of species to respond to selection when the environment changes. Moreover, a long-term study of the Soay sheep *Ovis aries* finds environmental variation to induce a negative correlation between selection and genetic variance [33]. Under harsh environmental conditions, selection is strong but genetic variance is low, whereas the opposite occurs under good conditions [33]. Thus, the potential rate of evolution is limited under variable environmental conditions, either by a lack of heritable variation or by relaxed selection.

Box 3. Does sexual selection erode genetic diversity?

Evolution depends not only on selection but also on additive genetic variance. Because sexual selection generally increases mating skew, thus reducing effective population size, sexual selection could erode genetic diversity and hence reduce the potential for evolutionary change [78].

A relaxation of sexual selection at the time of environmental change, which has been demonstrated in some systems [9,30,65], could diminish the erosion of genetic variation and maintain the potential for adaptation. Changes in the environment could also cause the optimal phenotype to vary in space or time and induce fluctuating selection. This could contribute to genetic diversity, depending on how genotypes map to phenotypes in different environments [79]. An increasing number of studies find genotype-by-environment interactions to maintain additive genetic variation in sexually selected traits, by preventing one variant from producing the optimal phenotype across all environments [13,80,81]. Different genotypes could then be favoured in different environments. For example, inbred lines of the lesser waxmoth *Achroia grisella* that are kept under three different competitive environments differ in their level of phenotypic plasticity for song attractiveness, condition and development rate [79].

Interestingly, a recent study suggests that climatic variation could increase genetic diversity by increasing the effective size of a population. In the grey seals *Halichoerus grypus*, the proportion of males that contribute to the effective population size depends on local weather conditions. More variable conditions lead to a broader range of males contributing genetically to the next generation [82]. This suggests that environmental variation could, in fact, increase genetic variation and thereby counteract the erosion of genetic variation through sexual selection.

Few studies have, however, empirically investigated how sexual selection influences the rate of adaptation. A comparative study on avian spring migration suggests that sexual selection facilitates adaptation to global warming. Species experiencing strong sexual selection have advanced their spring arrival to a greater extent than species experiencing weaker sexual selection [34]. The advancement is probably due to global warming relaxing survival selection against early arrival, allowing sexual selection to favour earlier arrival through female choice [34]. However, whether the advancement in spring arrival is a plastic response or reflects microevolution is unknown.

By contrast, most experimental studies where populations have been allowed to adapt to new environments in the presence or absence of sexual selection have found either no effect or a negative effect of sexual selection on adaptation. When replicate populations of *D. melanogaster* were allowed to adapt to low-grade thermal stress, with or without sexual selection operating, no influence of sexual selection on the rate of adaptation was detected [35]. Similarly, a more powerful design that included a treatment involving sexual selection alone revealed no benefit of sexual selection in the adaptation of *Drosophila serrata* to a novel food [3]. On the contrary, sexual selection imposed a direct cost on females, probably arising from male-induced harm. In the seed beetle *Callosobruchus maculateus*, sexual selection weakly accelerated adaptation to a novel host, by reinforcing natural selection, but depressed offspring production when the population was close to its adaptive peak, probably owing to intense sexual conflict [36]. Thus, contrasting results have been gained. The majority of studies suggest that sexual selection plays at most a weak role in adaptation to new conditions and could even have a negative effect on population viability through sexual conflict.

The importance of the rate and stage of environmental change

Although most empirical work suggests that sexual selection plays a minor role or a negative role during initial adaptation to changed conditions, several studies at later stages of adaptation find sexual selection to play an important role in divergence and in speciation [37–42]. In particular, sexual selection has been found to promote ecologically based divergence through directional selection in different directions in different environments [37–39,43]. For example, the dewlap design of the lizard *Anolis cristatellus* has diverged between populations to enhance signal visibility; dewlaps from xeric habitats are darker and dewlaps from mesic habitats are brighter [44]. Similarly, human disturbance of the African rain forest has caused divergence in plumage colour and song of the little greenbul *Andropadus virens* inhabiting mature and secondary forests, probably owing to changed signal propagation in the human-altered habitat [45]. Sexually antagonistic coevolution, in particular, could accelerate speciation, because the conflict of interest between males and females can result in rapid coevolution between harming males and resisting females, eventually causing reproductive isolation between allopatric populations [46,47].

The rate of environmental change and the time that has passed since the change occurred could consequently influence the effect of sexual selection on the rate of adaptation. Sexual selection appears to be maladaptive under sudden changes, but could be adaptive once sexually selected traits have started to evolve and become adjusted to the new conditions [43]. The history of the population and whether it has evolved in a stable or a variable environment could further influence the degree of plasticity in sexual traits and hence the ability of populations to adjust to environmental change. So far, no studies have empirically studied the effect of the rate or scale of environmental change on the process of sexual selection and its influence on population viability. Moreover, the effect of variation on the strength and form of sexual selection at different stages of adaptation deserves more attention. More research is needed on these topics.

Can sexual selection increase extinction risk?

If populations are not able to adapt to new conditions, they will eventually perish. The influence that sexual selection can have in the process is debatable [48]. Increases in the fitness costs of sexually selected traits under changed environmental conditions could reduce the overall reproductive output of the population. If the decline is too fast for other selective forces to rescue the population, then this could, in the worst case, lead to extinction [16,48–50]. However, sexually selected traits are often phenotypically plastic and subject to frequency-dependent selection, and the cost could therefore be adjusted to local conditions [51]. This could prevent the cost from rising to detrimental levels. Moreover, the feedback between population density and sexual selection could stabilise the level of conflict and prevent extinctions, as discussed above [26,52].

Overall, contradictory results have been reached. Early studies on the introduction success of birds, where species experience new environments, found indications that sexual selection might increase extinction risk [53–55]. However, later studies, based on larger data sets and controlling for introduction effort, have not found such an association [56,57]. Similarly, no correlation between the degree of sexual dimorphism and invasion success to new environments has been found for birds and fish, and only a negligible correlation has been observed for mammals [58]. In general, sexual selection has been found to be positively correlated with extinction risk in North American birds [59,60] but not in European birds [61] or in mammals [62]. As a notable exception, a study on the common lizard *Lacerta vivipara* suggests that sexual selection can increase extinction risk. In this species, male sexual behaviour is harmful to females and an excess of males in a population severely threatens population viability [63].

Thus, if sexual selection plays a role in increasing extinction risk under environmental change, the effect appears to be weak relative to other forces. However, when investigating the general effect of sexual selection on extinction, the data could be skewed if the most vulnerable species have already gone extinct [64]. Moreover, sexual selection could promote speciation, which could mask the effect of sexual selection on extinction and species diversity over evolutionary time.

Conclusions and future directions

Sexual selection is one of the major forces of evolution, but its effects on population viability and adaptation to new conditions are largely unknown. There is little evidence for sexual selection accelerating adaptation to new conditions. Instead, most empirical studies suggest that sexual selection is either relaxed or alternatively maladaptive during the initial stages of adaptation. However, once sexually selected traits start to evolve in response to new conditions, sexual selection in interplay with viability selection could play a crucial role in ecologically based divergence.

Phenotypic plasticity and particularly genotype-by-environment interactions in the expression of sexual traits could accelerate or slow down the rate of adaptation, depending on how the costs and benefits of the sexual traits, and hence their adaptive value, change. Little is known, however, about the effect of plasticity in sexual traits on the rate of adaptation. Similarly, the importance of other factors that could prevent the costs of sexual traits from increasing to detrimental levels under changed conditions, such as density dependence in the strength of sexual selection, is unknown.

More work is also needed on how additive genetic variance in sexual traits changes under environmental change, because this determines the possibility of adaptation. Further, the rate and scale of environmental change, and the history of the population, should have a decisive effect on the ability of populations to adapt through sexual selection. However, this has been largely unexplored, despite the fact that environments are presently changing at an accelerating pace owing to human activities. It is likely that sexual selection has its strongest negative effect on population viability under rapidly changing conditions, because there might not be enough time available for the costs of sexual traits to be adjusted to the new conditions.

At a more theoretical level, the effects of different forms of sexual selection in adaptation to new conditions, that is, whether they are dominated by good genes, compatibility genes, Fisher's process or antagonistic coevolution, are generally unknown. Because there are no population benefits involved in the Fisherian process or sexually antagonistic coevolution, sexual selection that is mainly driven by these processes might be a burden under environment change. Here too, more theoretical and empirical work is needed.

Overall, the role of sexual selection in modulating the response of populations to environmental change is far from clear. Equivocal results have been gained, and the effects of factors that influence the process, such as phenotypic plasticity, changes in additive genetic variance and the rate, stage and scale of environmental change, still need to be clarified. Finally, if the importance of sexual selection changes when environmental conditions are altered, then this could influence the strength and effect of natural selection at other selection stages. The effects of all selective forces, including sexual selection, need to be unravelled before we can predict the future of populations and manage endangered species under changing environmental conditions.

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