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Author for correspondence:
Michael D. Jennions
e-mail: michael.jennions@anu.edu.au

Sexual selection, phenotypic plasticity and female reproductive output

Rebecca J. Fox[1], Lutz Fromhage[2] and Michael D. Jennions[1]

[1]Division of Ecology and Evolution, Research School of Biology, Australian National University, Canberra, Australian Capital Territory 2601, Australia
[2]Department of Biological and Environmental Science, University of Jyvaskyla, PO Box 35, Jyvaskyla 40014, Finland

RJF, 0000-0003-3442-4189; MDJ, 0000-0001-9221-2788

In a rapidly changing environment, does sexual selection on males elevate a population's reproductive output? If so, does phenotypic plasticity enhance or diminish any such effect? We outline two routes by which sexual selection can influence the reproductive output of a population: a genetic correlation between male sexual competitiveness and female lifetime reproductive success; and direct effects of males on females' breeding success. We then discuss how phenotypic plasticity of sexually selected male traits and/or female responses (e.g. plasticity in mate choice), as the environment changes, might influence how sexual selection affects a population's reproductive output. Two key points emerge. First, condition-dependent expression of male sexual traits makes it likely that sexual selection increases female fitness *if* reproductively successful males disproportionately transfer genes that are under natural selection in both sexes, such as genes for foraging efficiency. Condition-dependence is a form of phenotypic plasticity if some of the variation in net resource acquisition and assimilation is attributable to the environment rather than solely genetic in origin. Second, the optimal allocation of resources into different condition-dependent traits depends on their marginal fitness gains. As male condition improves, this can therefore increase or, though rarely highlighted, actually decrease the expression of sexually selected traits. It is therefore crucial to understand how condition determines male allocation of resources to different sexually selected traits that vary in their immediate effects on female reproductive output (e.g. ornaments versus coercive behaviour). In addition, changes in the distribution of condition among males as the environment shifts could reduce phenotypic variance in certain male traits, thereby reducing the strength of sexual selection imposed by females. Studies of adaptive evolution under rapid environmental change should consider the possibility that phenotypic plasticity of sexually selected male traits, even if it elevates male fitness, could have a negative effect on female reproductive output, thereby increasing the risk of population extinction.

This article is part of the theme issue 'The role of plasticity in phenotypic adaptation to rapid environmental change'.

1. Introduction

Sexual selection favours traits that are often exclusively expressed or only exaggerated in males, such as weapons and ornaments, which increase mating or fertilization success when there is competition for mates or fertilization opportunities. In contrast, natural selection favours economically efficient traits that are usually similarly expressed in both sexes, which improve foraging ability, predator evasion, disease resistance and so on. In general, therefore, natural and sexual selection are in opposition. There is a trade-off between a longer life or a faster mating rate (but see [1,2]). It might therefore seem slightly paradoxical that researchers have asked whether sexual selection on males can increase the rate at which females adapt to a novel environment [3–7]. This is akin to asking if sexual selection on *males* elevates the mean absolute lifetime

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reproductive output of *females* (i.e. population mean fitness (definition modified from [8]; see also [9])), thereby increasing the maximum population growth rate and decreasing the likelihood of population extinction. In a similar vein, researchers studying phenotypic plasticity, especially those motivated by conservation concerns arising from climate change, industrial-scale agriculture and urbanization, have asked whether plastic responses to rapid environmental change reduce the likelihood of population extinction ('plastic rescue' *sensu* [8]) because phenotypic plasticity increases population mean fitness [10].

Surprisingly, these two research questions are rarely combined. Researchers studying plastic rescue mostly ask whether plastic responses of naturally selected traits to a changing environment are broadly adaptive (i.e. elevate male and female absolute fitness). It is rare for them to instead ask whether adaptive plasticity of sexually selected traits in *males* (i.e. those that increase relative mating or fertilization success) will increase the mean absolute lifetime reproductive output of *females*. Before proceeding further, we should acknowledge that mean *female* lifetime reproductive success (LRS) is an imperfect proxy for the realized growth of a population and its effective population size (the two key demographic parameters that influence extinction risk (review: [11]; see also [12])). We are essentially assuming there is 'hard' rather than 'soft' selection on female LRS (see [13]) such that *absolute* differences in female LRS between a population with and without sexual selection translate into differential recruitment rates. This is a simplification, but one that is widely used when investigating so-called 'population fitness' (e.g. [8]).

Many factors select for different levels of expression of sexually selected traits by males (review: [14]). For example, the sonic and light environment affect the transmission of acoustic and visual courtship signals respectively (review: [15]); and the local predator and parasite community determine the costs of investing in attractive traits that increase a male's vulnerability to predators, or capacity to tolerate parasites. The benefits of investing in sexually rather than naturally selected traits also depend on the strength of sexual selection, which can covary with the operational sex ratio, density of competitors and mate encounter rate [16–18]. Perhaps the most important and widespread form of phenotypic plasticity in sexually selected traits relates to the availability of resources. Many sexually selected traits show 'condition-dependent' expression, being smaller when food is limited. All of these factors should select for males that detect appropriate environmental cues and show an adaptive plastic response in their investment into sexually selected traits.

In this review, we explore how plastic responses by males to a changing/novel environment could influence the mean absolute LRS of females, and hence the likelihood of population extinction. We focus on plasticity in males rather than females because theory suggests that sexual selection mainly acts on males [19–21]. This claim is widely supported empirically by greater male weaponry and ornamentation [22–25], and by a stronger relationship in males than females between mating and reproductive success ([26]; but see [27,28]) (for examples of sexual selection in females see [29,30]).

Terminology: We define *phenotypic plasticity* as a genotype producing different phenotypes depending on the environment in which it is expressed. This is broadly synonymous with individuals (whose genotype is constant) showing a *plastic response*. The response is adaptive if it increases fitness compared with continued expression of the phenotype produced prior to the environmental change of interest. When referring to the degree of plasticity expressed by a genotype we refer to its *reaction norm* (the function relating the expression of the focal trait to an environmental parameter). Selection for an adaptive plastic response is synonymous with selection for an appropriately shaped reaction norm. Evolution of plasticity can only occur if there is additive genetic variation in reaction norms (i.e. gene-by-environment (G × E) effects). We should note that individual plasticity is not strictly synonymous with G × E, despite individuals having different genotypes, because individuals might vary phenotypically across focal environments for purely non-genetic reasons (e.g. a good start in life might increase their ability to adjust their phenotype (permanent environment effects: see [31])).

2. How can sexual selection affect female reproductive output?

Regardless of whether or not phenotypic plasticity in sexually selected traits is adaptive for males, it seems unlikely on the face of it to affect the likelihood of population extinction in a rapidly changing environment. This is because the expression of sexually selected traits simply determines which males mate. *Does this have any bearing on how many females there are, how often they breed, and the success of each breeding attempt?* Sexual selection on males will only influence population extinction if it affects these three key demographic parameters. We therefore first address the role of sexual selection in determining female LRS before we consider additional compounding effects of male plasticity. Naively we might assume that males cannot affect mean female LRS because females are rarely limited in their ability to acquire a mate, but this conclusion would be wrong [32]. Males can affect mean female LRS for three main reasons.

(a) There is a positive genetic correlation because successful males transfer genes that elevate their daughters' LRS (r_G) [33,34]. This is most likely to occur when there is additive genetic variation for naturally selected genes that determine condition, and male sexual traits are condition-dependent (see §4). Conversely, there could be a negative correlation if successful males transfer sexually antagonistic genes that elevate their sons' mating success but lower their daughters' LRS [35,36]. A negative inter-sex genetic correlation (r_{MF}) for fitness has been documented in several species [37–41], but this is not strictly equivalent to a negative genetic correlation between male sexual competitiveness and female LRS. For example, even in the absence of sexual selection, a negative r_{MF} could arise if natural selection favours different genotypes in each sex, which is likely given sex-specific life histories (e.g. [42–44]). Strictly speaking it is necessary to measure the genetic correlation (r_G) between male and female fitness that is attributable to sexual and natural selection respectively. This correlation is likely to vary predictably depending on the environment in which it is measured [45,46] (see §5). It should also be noted that a positive r_G is not equivalent to female choice for genetic quality ('good genes'), as this refers to a sire's effect on mean offspring fitness (i.e. daughters *and* sons) [47–49].

(b) There is a phenotypic correlation (r_P), between a male's mating success and his mate's LRS because male sexual competitiveness covaries with: (i) traits that determine the level of sexual conflict over mating and sperm use (e.g. seminal toxins, traumatic damage to females) [50–52]; (ii) the likelihood he passes on sexually transmitted infections [53,54]; (iii) the quantity and/or quality of resources transferred (e.g. parental care, nuptial gifts) that improve a female's ability to rear viable offspring [55–57]; and, (iv) his daughters' LRS due to his rate of 'offspring provisioning' (e.g. food intake when young, or access to breeding resources as an adult) (e.g. [58,59]). When calculating the contribution of successful males to a population's reproductive output we need to determine how many daughters they sire compared with the average male, and if their daughters are of above average fecundity [60]. In general, however, there is only weak empirical evidence that sire attractiveness affects the offspring sex ratio [61].

(c) Even if we ignore the issues of which males mate, male–male competition leads to the coevolution of sexually selected male traits and corresponding female traits (e.g. mate choice, mating resistance) that generally reduce female LRS below the level that would occur in their absence [62]. First, investment into sexual traits lowers males' parental investment, reducing the mean output per breeding event [21]. Second, intense sperm competition can cause sperm depletion, which lowers fertilization success, reducing the output per breeding event. This is most common when only a subset of males acquire mates [63,64]. Third, sexual conflict that arises when females evade and resist males tends to increase the interval between breeding events, and lowers female fecundity owing to energetic costs, lost foraging time and allocation of resources to defensive traits instead of offspring [65–67]. Sexual conflict can also kill females, reducing the number of breeding females in a population [68,69].

3. The net effect of sexual selection on mean female reproductive output

For all of the scenarios covered in §2(a,b) there are both theoretical models and empirical data suggesting that mating with more successful (i.e. competitive) males can have either a positive or negative effect on mean female LRS, depending on contingent factors. For example, the proportion of genes with sexually antagonistic effects tends to be lower when populations are in a novel or changing environment (e.g. [70–72]) (§5). Consequently, there is no consensus as to how variation in male mating success due to sexual selection affects the likelihood of population extinction. In contrast, all of the sexually selected processes in §2(c) reduce mean female LRS. The net effect of sexual selection on mean female LRS, hence population extinction risk, is therefore uncertain [3–7], although it seems on balance to be beneficial.

First, sexual selection is positively correlated with lineage diversification (speciation minus extinction rates) across many taxa ([73,74]; but see [75,76]). If this relationship is partly driven by lower extinction rates, it is plausible that sexual selection has a beneficial effect on mean female LRS. Second, a recent study of ostracods found that persistence in the fossil record (i.e. time to extinction) was shorter for species assumed to have more intense sexual selection on males [77]. Third, numerous experimental evolution studies have created breeding lines in which sexual selection is either present (females have access to many males) or absent (enforced monogamy). The two types of lines often evolve differences in female fecundity, lifespan, offspring viability and other traits (review: [78]). Sexual selection clearly elevates components of female LRS in some studies (e.g. [79–81]) but not others (e.g. [82–84]). Intriguingly, a few studies have directly shown that sexual selection lowers the rate of line extinction [85–88].

4. Environmental drivers of plasticity in sexually selected male traits

In §2 we noted that sexually selected male traits can vary in the costs they impose on female LRS (e.g. ornaments versus seminal toxins). A key challenge in understanding how plasticity affects population extinction risk is therefore to predict how males plastically allocate resources into different sexually selected traits as the environment changes. We defer discussion of this topic to §6. In this section, we simply introduce three key factors that induce plasticity in sexually selected traits: environment-dependent resource availability, the social environment and the signalling environment. We emphasize the benefits to males of these plastic responses with the implicit understanding that whether they are adaptive or not also depends on the costs of developmental/cognitive mechanisms that allow for plasticity, the capacity to detect environmental cues, and the likelihood of misinterpreting these cues [89–92]. See [10] for a more complete discussion of the costs of plasticity in the context of adaptation to novel environments.

(a) Condition-dependence traits: a plastic response to resource availability

'Condition' is defined as the acquired resources that an individual can strategically allocate to life-history traits [93]. Condition is a simple concept invoked in numerous sexual selection models [49,94,95], but it is notoriously difficult to measure [96,97]. Nonetheless, it is often stated that most sexually selected traits are strongly condition-dependent [98–100]. This claim is based on trait expression positively covarying with environmental variation in resource availability, and this covariation being stronger for sexually than naturally selected traits [97,101] (e.g. a greater change in sexually than naturally selected traits when diet is manipulated). It remains unclear to us whether other key life-history traits (e.g. immunocompetence, female fecundity) are, in fact, less condition-dependent than sexually selected male traits (reviewed by [98]; but see [99,102]). Nonetheless, phenotypic plasticity in sexually selected traits attributable to environmental variation in resource availability is often high. This is consistent with a zero-sum game in which success at competing for mates and eggs is largely determined by a male's relative investment in attractiveness, fighting ability and sperm competitiveness [103,104].

Variation in condition among individuals arises owing to contingent external factors (e.g. season of birth, which affects resource availability in the environment) and direct effects of many naturally selected traits that determine the ability to acquire or assimilate resources (e.g. foraging ability, immune function). Strictly speaking we cannot treat condition-dependence as synonymous with phenotypic plasticity. Why? Plasticity involves a change in trait expression for a given genotype due to the environment. In contrast, condition-dependence could reflect differences in the resources that can be allocated to a trait that arise solely from genetic differences among individuals rather than environmental factors. However, we think it is biologically sensible to assume that phenotypic variation in condition-dependence traits arises owing to both genetic and environmental variation. In addition, we assume that condition-dependence is almost always associated with G × E interactions (hence additive genetic variation in reaction norms) when considering large environmental changes, because when the environment changes in unexpected directions it seems likely that only some of the existing standing genetic variation will yield phenotypes that improve an individual's fit to the environment and thereby increase condition.

Crucially, variation in condition among males is 'revealed' in condition-dependent, sexually selected traits. So male mating success is potentially correlated with additive genetic variation for naturally selected traits that benefit females, thereby making r_G positive if condition-enhancing genes elevate both male mating success and female LRS. Phrased slightly differently, condition-dependent traits provide a mechanism whereby sexual selection can eliminate deleterious alleles from a population, regardless of whether they arise owing to mutations, gene flow between locally adapted populations [13,105,106], or mismatch due to environmental change ([5,107]; but see [108]). The existence of condition-dependent, sexually selected male traits might therefore seem likely to elevate mean female LRS because of the genetic benefits to females of mating with males in good condition. Unfortunately, this conclusion is premature because many condition-dependent traits also damage females as a by-product of conferring an advantage to males when there is sexual conflict over mating (e.g. [109]). This makes it crucial to know how males allocate resources to different condition-dependent traits as resource availability changes owing to the environment (see §6).

(b) The social environment: the response to cues of sexual competition

Males could benefit from plastic responses of sexually selected traits to the number of competitors, the sex ratio, and other social factors that affect the compound probability of obtaining a mate and their sperm achieving fertilization. The most common plastic responses are shifts in sperm production, ejaculate size, and rates of courtship or aggression [63,110–114]. Studies that examine plastic responses to the social environment by males rarely quantify the effect on female reproductive output ([115,116]; but see [117]). Instead, researchers usually extrapolate from effects of male traits on females in other studies to predict how male plasticity will alter female LRS. For example, male *Drosophila* that perceive higher rates of sperm competition mate for longer and stimulate higher rates of egg laying [118]. All else being equal, this implies that male plasticity might elevate female LRS, but this is obviously contingent on the mortality costs to females of a male-induced increase in productivity (e.g. [119]). In other studies, male plasticity seems likely to reduce female LRS. For example, dominant males in domestic fowl mate more often and produce more sperm than subordinates but, unlike subordinates, ejaculate quality decreases over successive copulations [120]. Greater investment into sperm in a more competitive social environment could therefore lower female LRS if it reduces egg fertilization rates.

Our understanding of how plastic response of males to social cues affect female LRS is limited. In some cases, we can use theory to reliably predict plastic responses in specific male traits (e.g. strategic ejaculation [113]). In other cases, the plastic response is not in the predicted direction. For example, there were no consistent effects of perceived future mating opportunities on investment into either pre or post-copulatory sexual traits by guppies [121]; nor did male mice adjust their ejaculates to the number of potential mating opportunities, although they did so in response to the perceived risk of sperm competition [122]. These anomalies might arise because the marginal benefits of allocating resources to different sexually selected traits depend on the level of mating and fertilization competition [114]. Again, this means it is crucial to be able to predict how males allocate resources to different traits if we want to relate male plasticity to female LRS (§6).

(c) The signalling environment

There is good evidence, especially in species where males call to attract females, that males adjust their signals to the transmission properties of the environment. These are often textbook examples of adaptive plasticity. For example, studies show that anthropogenic factors, such as urban noise and artificial lighting, impose direct selection on sexually selected male traits [123,124]. Numerous studies have further reported differences between urban and rural populations in sexually selected traits, such as bird song ([125,126]; review: [127]). Many of these differences are in the direction predicted by functional considerations about signal transmission efficacy [128]. It seems improbable that selection on male genetic variation in song imposed by urban noise is responsible for urban–rural population differences (but see [129]). Given the recent origin of cities, these differences instead implicate plastic responses due to learning, and even cultural evolution. In general, it seems unlikely that male plasticity in response to the signalling environment will affect mean female LRS. It might, however, reduce female mate search costs by increasing males' conspicuousness; and it could make it easier to discriminate between potential mates, which would increase the strength of sexual selection which can then affect female LRS (§5).

5. Male plasticity and female reproductive output due to the genetic correlation (r_G)

So far, we have broadly discussed how sexual selection might affect female LRS (§§2 and 3), and then described the main types of plastic responses of male sexual traits (§4). Next, we ask how male plasticity affects mean female LRS, hence population extinction (§1), driven by the genetic correlation (r_G) between non-random male mating success due to the expression of sexually selected traits and female LRS. We mainly emphasize the role of condition-dependence (i.e.

plasticity when due to the environment) in male sexually selected traits.

In general terms the observed phenotypic response to selection (R) of a trait in a two-trait system is

$$R_x = h_x^2 S_x + r_{xy} h_x h_y S_y, \tag{5.1}$$

where $h^2 = V_{\mathrm{A}}/V_{\mathrm{Phenotype}}$ = heritability, and S = selection differential.

Here we can think of x = female LRS, y = male mating success, so $r_{xy} = r_{\mathrm{G}}$ (equations 11.6 and 19.3 in [130]). If the genetic correlation (r_{G}) between female LRS and male sexual competitiveness is positive then non-random mating due to sexual selection on males hastens the fixation of genes that improve female LRS above that due to natural selection on female LRS. The magnitude of r_{G} depends on the additive genetic variation (V_{A}) in male mating success and female LRS and their covariation ($r = \mathrm{covar}(x, y)/\surd[\mathrm{var}(x)\mathrm{var}(y)]$), while the correlated response to selection on male mating success on female LRS due to a non-zero r_{G} also depends on the heritability of male mating success. If sexual selection is weak (i.e. variation in mating success is mainly due to chance) then there is little difference between mean male mating success and the mating success of those males that breed, so S for mating success is small; and the heritability of male mating success is also low because there is no effect of genetic variation in sexual competitiveness on male mating success. In the absence of sexual selection, a positive r_{G} has no effect on female LRS. Simply put, if females mate randomly they do not disproportionately mate with males with genes that elevate female LRS, even if $r_{\mathrm{G}} = 1$.

Given condition-dependent expression of sexually selected male traits, theory suggests that r_{G} is more positive in a novel or rapidly changing environment, as both sexes tend to have phenotypes that are similarly displaced from their selected optima (figure 1*a*). Genes under natural selection in males are therefore likely to benefit females because they will equally move females towards their new optimum. If so, the inter-sex genetic correlation for fitness (r_{MF}) is positive [45,46]. More specifically for r_{G}, some of the V_{A} in condition-dependent, sexually selected male traits that determine male success is due to genes that otherwise improve naturally selected traits (§4). As such, more competitive males carry genes that tend to elevate mean female LRS if natural selection acts concordantly on both sexes; hence $r_{\mathrm{G}} > 0$. In contrast, in a stable environment, genes that are under consistent selection in both males and females (e.g. genes for condition) tend to reach fixation. The V_{A} in condition is then reduced so that a greater proportion of the standing additive genetic variation in LRS and male mating success is attributable to sexually antagonistic genes; hence $r_{\mathrm{G}} < 0$. Studies that compare r_{MF} (often, but not always, identical to r_{G}; see §2) between populations that are either well or poorly adapted to the local environment suggest that r_{MF} is more positive in novel environments ([34,70,131]; but see [132–134]), although a full meta-analysis is still needed. Of course, several key assumptions underlie the claim that r_{G} is more often positive in novel environments [34,46,108].

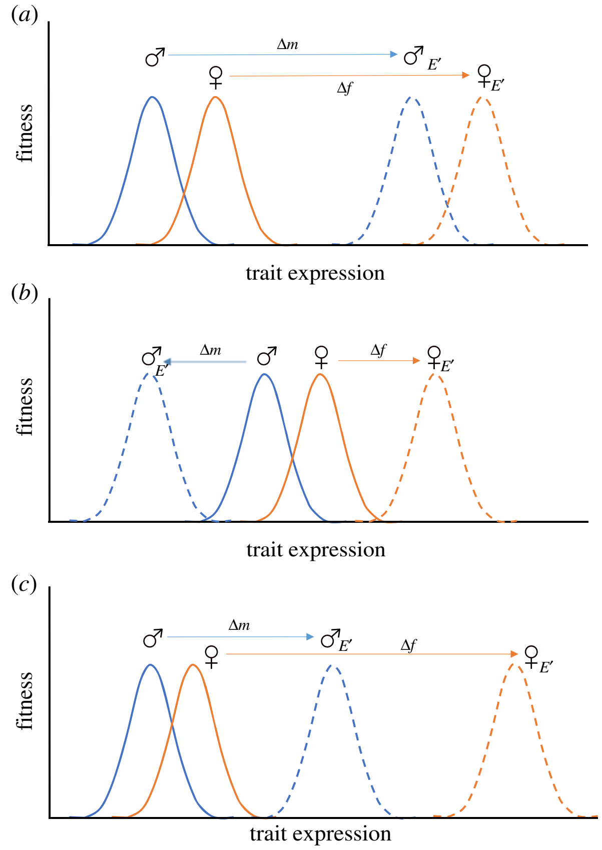

Figure 1. The likely change in the intersex genetic correlation for fitness (r_{MF}) in a changed environment. In the original environment, phenotypic values for males (solid blue) and females (solid orange) are distributed around sex-specific fitness optima. Owing to opposing selection, and in the absence of sex-limited gene expression, the mean phenotype is likely to lie between the two optima. In a novel environment (E'), trait optima for each sex shift and, following selection, phenotypic values are eventually distributed around the new optima for males (dashed blue) and females (dashed orange). (*a*) Shows the 'classic' case in which both sexes are displaced in the same direction and by the same amount ($\Delta m = \Delta f$). Genes under natural selection in males are therefore likely to benefit females and the inter-sex genetic correlation for fitness (r_{MF}) is positive. In (*b*) the novel environment causes the new trait optima for each sex to shift in opposite directions (here $\Delta m = \Delta f$, but with opposite signs), resulting in greater intra-locus sexual conflict, i.e. r_{MF} is negative. Finally, (*c*) represents a case in which the new sex-specific optima are displaced in the same direction, but by different amounts (here $\Delta m < \Delta f$), such that r_{MF}, while briefly positive, becomes more negative the further the mean trait value in the population surpasses the new male optimum.

First, if additive genetic variance changes owing to gene-by-environment (G × E) interactions [134], this can affect r_{G} or r_{MF} in unexpected ways. To take an extreme case, $r_{\mathrm{G}} = 0$ if there is no additive genetic variation in male mating success in a new environment where chance alone determines which males mate. For example, consider what happens in the case of a sexually dichromatic cichlid fish with female mate-choice based on male colour that lives in clear water if the environment becomes highly turbid [135–137]. Even if condition still determines male coloration, bright males do not have higher mating success and the link between condition, which still elevates female LRS, and male mating success is broken. Second, sex-specific optima in a novel environment might be associated with greater intra-locus sexual conflict. For example, consider a population with a mean phenotype for a naturally selected trait that is intermediate between the male and female optima. A standard assumption is that, in the novel environment, the trait optima are displaced in the same direction for both sexes [138] (figure 1*a*). If, however, they are displaced in opposite directions then the potential for intra-locus sexual conflict will increase (figure 1*b*; see also fig. 1 in [134]). Even if the new sex-specific optima are displaced in the same direction, if they are further apart in the novel environment then r_G will tend to be more negative once the population mean trait exceeds the new optimum of one sex (figure 1*c*). Third, even if sex-specific optima are minimally displaced, there could be greater sexual antagonism in a novel environment owing to sex-specific G × E interactions. For example, a genotype beneficial to both sexes in the original environment could produce a phenotype that is displaced much further from the female than male optimum in the novel environment. This is plausible given that a novel environment might affect sex-specific life histories (i.e. the sexes differ more in the particular traits that increase their condition owing to, for example, greater sex differences in the available prey types). The interested reader is referred to [108] for a useful summary of other ways in which r_{MF}, r_G (and S) might be affected by a changing environment.

So what role does male plasticity play in increasing the extent to which sexual selection on males increases female LRS in a novel environment? Unfortunately, most theoretical studies of how sexual selection facilitates adaptation implicitly assume that sexually selected traits are condition-dependent. This is because it is the only obvious mechanism to link the process of females disproportionately mating with males with greater investment in sexually selected traits (usually modelled assuming female choice) to genetic benefits that elevate female reproductive success [13,45,46,106]. However, this approach precludes answering the broader question of whether r_G is more positive, sexual trait heritability ($h^2 = V_A/V_P$) is higher, or S is larger in a novel environment if sexually selected traits are phenotypically plastic instead of fixed in expression (i.e. whether they increase the value of $r_{xy}h_xh_yS_y$ in equation (5.1)). We can, however, still ask how sexually selected male traits being condition-dependent might affect the values of these three key parameters when the environmental changes. It is worth noting here that each of these terms incorporates elements of the other so they are not independent (e.g. V_A affects the value of r_G and $h^2_{\text{male mating}}$; and $h^2_{\text{male mating}}$ incorporates an element of S, i.e. if $S = 0$ then $h^2_{\text{male mating}} = 0$).

(a) Plasticity and the heritability of male mating success

Condition-dependence implies that the environment affects phenotypic variation in sexually selected male traits, hence sexual competitiveness, and mating success. The degree of phenotypic displacement of the average male from the naturally selected optimum in a novel environment is likely to affect the distribution of male condition, hence V_P ([102], fig. 1 in [134]). Males will generally be in poorer condition, and the resultant decline in mean condition is likely to be associated with greater variation in condition (see [108,139]). This implies that male mating success has lower heritability in a novel environment owing to the larger V_P, but heritability (V_A/V_P) also depends on V_A. Additive genetic variation in condition, hence sexual trait expression, is likely to change in unpredictable ways in a novel environment simply because of G × E interactions. This makes it unlikely that we can predict how condition-dependence will affect heritability. There is, however, some evidence from meta-analyses that heritability is lower in less favourable environments, although this is contingent on the type of trait being measured [140]. One explanation for lower heritability of condition in less favourable environments (i.e. when extractable resource availability is lower owing to maladaptation) is that there is a minimum threshold below which individuals die, which reduces V_A for condition among surviving males.

(b) Plasticity and the strength of sexual selection

The strength of sexual selection affects both S and h for mating success in equation (5.1). The heritability of male mating success depends on non-random variation in mating success due to sexual selection on males (because this creates the necessary link between V_A in male sexually selected traits and mating success). We therefore need to know how a novel environment changes the types of males that females choose, and what factors determine which males win fights, or have greater sperm competitiveness.

Initially, greater V_P for male condition in a novel environment seems likely to increase the strength of selection S because the contrast between high and low condition males is exacerbated. But this need not be the case. For example, the extent to which choosy females discriminate between males based on ornament size might decline when the mean ornament size is smaller owing to males being maladapted and in poorer condition. This could occur if females use size-based threshold rules to determine which males are suitable mates: if most males fall below the threshold, they will be equally (un)attractive as mates. More generally, phenotypic variance in traits depends on how resources are allocated to different sexually and naturally selected traits. The relationship between the mean condition of males and how males allocate resources to different condition-dependent traits is hard to predict (§6). Plastic shifts in allocation, even if only among sexually selected traits, could lead to unexpected outcomes. These include males in better condition being less successful because plastic responses are maladaptive in the novel environment. This is plausible because these responses have evolved based on females' behaviour in the original environment. For example, greater investment into ejaculate size by males in better condition might be disadvantageous if females in a novel environment do not mate multiply. In sum, condition-dependent changes in allocation could alter V_P in key sexually selected traits in ways that change the proportion of variation in mating and fertilization success that is attributable to V_A in condition, thereby reducing the variation in male mating success, which also increases female LRS. Similar adverse outcomes for female LRS could arise when males plastically respond to cues about the social, or even signalling, environment that alter covariation between V_A in condition and male mating success.

Another way that male plasticity could weaken sexual selection is if males respond to social cues by 'specializing' in increasing their success at certain stages of reproduction (e.g. mate acquisition versus fertilization). Here we note that, for ease, we previously treated sexual selection as synonymous with variation in mating success in equation (5.1). Strictly speaking we should refer to 'variation in fertilization success that arises from the combined effects of female mate choice, cryptic choice, the intensity of sperm competition, and how winning male–male contests elevates mating and fertilization success'. For brevity we do not. Specialization can reduce variation in male reproductive success under sexual competition if males make the 'best of a bad job' (e.g. small males or those in low condition sneak rather than court [141]). More generally, when males plastically adjust their investment in sexually selected traits to take advantage of information about individual females, this can reduce variation in male fitness. For example, males can plastically adjust ejaculate size based on cues about a female's previous mating history or the likelihood that she will re-mate [113].

Conversely, plasticity could increase V_P in male reproductive success under sexual competition. For example, a lack of detectable variation among males in one trait in a novel environment could favour females that shift their attention to assessing males using another trait ([135]; see also [142]). If males plastically adjust their investment into sexual traits that are still detectable by females [143], this could increase (or decrease) the variation in attractiveness among males depending on the ease with which females can discriminate among males for different trait–environment combinations. In general, although many studies have documented that plastic responses affect which males mate or sire offspring, far fewer studies have quantified how this affects the net strength of sexual selection on different male traits.

(c) Plasticity and r_G

To recap, r_G depends on V_A in male success under sexual competition, V_A in female LRS, and their covariation. We have already discussed how condition-dependence might affect V_A in male success via the heritability (V_A/V_P) of male success. However, we glossed over the possibility that the proportion of V_A in male success attributable to condition changes across environments. This will affect the covariation between male success and female LRS. For example, if most V_A in male success is due to sexually antagonistic genes then r_G will be negative. A major consideration is therefore how male plasticity, other than that due to condition-dependence, affects the proportion of V_A in sexually selected traits attributable to sexually antagonistic genes. To our knowledge, few empirical or theoretical studies have explored this question. For example, does plastic expression by males of sexually selected traits in response to changes in social cues, such as lower population density in a novel environment, decrease the likelihood that male sexual traits are associated with genes that elevate female LRS?

6. Direct effects of males on female reproductive output

Males with greater expression of certain sexually selected traits can either elevate or depress the LRS of their mates (via r_P) §2(a,b). For this to affect mean female LRS there must be sexual selection so that some males have higher mating success than others. More generally, sexual competition among males can affect female LRS irrespective of which males end up mating §2(c). Any effect of male plasticity on mean female LRS therefore depends on how it affects the strength of sexual selection and which male traits increase males' success (i.e. are they those that increase or decrease female LRS?). We have already discussed the strength of selection in §5 so we now focus on plastic changes in selected male traits.

First, it seems self-evident that the mixture of plastic responses by males to social cues, the signalling environment and the total resources they acquire and assimilate (i.e. condition) owing to being in a different environment makes it almost impossible to predict how resources will be allocated to different sexually and naturally selected traits. Less obvious, however, is the fact that it is still difficult to make predictions even if we only consider adaptive allocation of resources to different condition-dependent traits [95]. The adaptive response to an increase in condition driven by greater resource acquisition is to allocate these additional resources to the trait with the greatest marginal fitness gains. (In a novel environment, where fewer resources are available, we can treat this as a question of reduced investment into the trait where there will be the smallest marginal decrease in fitness.) This suggests that additional resources will be allocated exclusively to a single trait with the highest gain, such that only a single trait exhibits positive condition-dependence. There are, however, general reasons to believe that marginal fitness gains will not consistently differ among traits as a male's condition changes. First, investment into a trait often yields diminishing fitness gains. For example, whenever a trait increases the probability of a particular outcome, such as detection by potential mates, it cannot be increased beyond its maximum value of 1. Second, the marginal fitness gains from different traits are rarely independent. Fitness gains depend on the current values of other traits, and traits tend to function most efficiently if they are 'balanced' so that an individual operates as an integrated unit. For example, a longer tail ornament might be favoured by female choice, but it will eventually become so long that investment into larger wings to maintain the ability to fly is likely to be more advantageous than a further increase in tail size. This should lead to plastic responses with increased expression of multiple traits in environments where males have access to more resources. Third, some traits might become more efficient (hence have greater fitness gains) when expressed at a higher absolute level (e.g. [144]). If so, better condition could induce a shift in allocation that manifests as an increase in the focal trait, alongside a *decrease* in other (fitness-enhancing) traits [95]. This is one reason why both acquisition and allocation are themselves sometimes described as condition-dependent (e.g. [145]).

Clearly, the sheer number of possible plastic responses by males to a change in condition that arise from being in a novel environment makes general predictions about plasticity in specific sexually selected traits problematic. There is no guarantee that greater condition leads to equal increases in all condition-dependent sexually (or naturally) selected traits. Broadly speaking, optimal condition-dependent allocation depends on the shape of the multivariate function that links traits to fitness. This function depends on species-specific details, such as morphological integration, the ecological context and, in the case of sexually selected traits, how the intensity and type of sexual selection (e.g. mating versus sperm competition) change with the environmental availability of resources that affect male and female condition. Consequently, when sexually selected traits vary in their effects on female LRS (e.g. a reduction in male song rate is unlikely to damage a female, while investment into seminal toxins is likely to induce female mortality), it is hard to determine whether condition-dependent plasticity will elevate or lower female LRS when males are in a novel (usually more stressful) environment.

When there are social cues about the level of mating or sperm competition there is often a clear theoretical prediction about how male investment will change for specific traits; and empirical studies typically report plastic responses in the predicted direction (i.e. greater investment in ejaculates as sperm competition increases) (review: [111]). However, as noted for condition-dependence, it is a challenge to predict the adaptive response when sexual selection acts on multiple traits. Specifically, the social setting could cause the marginal benefits of investment into different traits to change because of shifts in the relative importance of different sexual selection processes (e.g. courtship versus sperm competition). Even when models make predictions about optimal investment into testes versus weapons/ornaments in different social contexts (e.g. [94]), they are hard to test because: (a) there are simplifying assumptions about the constancy of natural selection that do not apply if the social setting affects naturally selected traits; (b) most models predict evolution due to changes in gene frequencies, rather than the optimal plastic response, but the two outcomes are not necessarily in agreement (§8); (c) there is within-population variation in condition. All these factors makes it harder to predict the optimal plastic response for each individual (for a similar problem see [95]).

Given no clear prediction about how males will allocate resources to different traits depending on their condition, determining the allocation patterns that are likely to arise in nature is chiefly an empirical matter. Even then, the relative amount of variation in acquisition versus allocation among individuals affects the observed population level correlations between traits ([146]; review: [145]). The two main areas with relevant data are: (a) whether condition-dependent male sexual signals are honest indicators of parental care, and (b) whether males with greater investment into sexually selected traits (preferred males, or males that win fights for access to females) benefit or harm their mating partners compared with the average male.

(a) A 'good parent' model suggests that condition-dependent sexual traits honestly signal parental care, while 'differential allocation' models predict that sexual selection on males lowers parental care owing to the resource trade-offs that males face [147–149]. This is why the relationship between condition-dependent male sexual signal and paternal care is unclear, and both outcomes seem possible [150]. However, the fact that female mating preferences might evolve in response to the direction of the relationship would appear to favour males being 'good parents', which could even lead to the evolution of male-only care [151]. But the enduring challenge is to explain why attractive males provide more care when mating precedes caring. In general, there must be inherent constraints on preferred males, perhaps owing to the social setting (e.g. strict monogamy [149], or because early mate desertion by females increases the value of male care [152]), such that males gain more by providing the 'advertised' care than redirecting resources to pursue additional mating opportunities (see also [56]). The extent to which such constraints are associated with plastic male responses to condition due to environmental variation is an open question, but it is one way in which plasticity could facilitate the process of sexual selection increasing mean female LRS. In general, there is high variation among species in the link between male sexual trait expression and how it affects female LRS through parental care, fertilization success, or other factors that influence female fecundity (e.g. nuptial gifts) [55].

(b) It seems unlikely that females would prefer males that lower their LRS, but this occurs in some species, and presumably reflects an on-going 'arms race' between seduction and resistance that males are currently 'winning' (e.g. [50,51,153]). Mating with males who are more sexually competitive can still increase a female's fitness even if it lowers her LRS if the costs of mating resistance are higher than accepting such males as mates. However, selection on females could lead to the evolution of the ability of females to reduce mating costs [154]. The net effect is that sexual selection on males can lower mean female LRS. But, to what extent does male plasticity influence this process? First, condition-dependent expression of damaging male traits might magnify the harmful effects of mating with more sexually competitive males. Intriguingly, however, we know of no systematic review that determines the extent to which, for example, experimental manipulation of male condition is associated with increased expression of specific male traits that appear to harm females, such as seminal toxins and genital structures (but see [155]). There is, however, evidence that social cues of the intensity of sperm competition lead to plastic responses in ejaculates (e.g. protein content and sperm count) that lower female LRS [122,156]. In addition, recent studies suggest that greater relatedness between competing males can result in phenotypic responses that reduce the extent to which males lower female LRS when competing for fertilizations (e.g. [157,158]).

7. Plasticity and females

We have emphasized sexual selection on males but, of course, sexual selection also acts on females (e.g. female–female competition for breeding opportunities and male mate choice) (reviews: [30,159,160]). What effect do sexually selected female traits have on mean female LRS? Clearly, mean female LRS must decline if there is any fitness trade-off with naturally selected traits [161]. If females simply used a lottery rather than expended resources on competition to determine contested breeding opportunities, then the 'winning' female could invest more in reproduction. Of course, the same is true for males, but a key difference is that the mean LRS of breeders is likely to be more strongly affected by which females, rather than males, breed. This claim is based on the assumption that there is greater variation in female fecundity and parental investment than in direct male effects on female LRS §2(b). A more interesting question is: to what extent does plasticity in sexually selected female traits increase the realized fecundity of breeders when breeding sites and/or male mates are a limited resource? If female investment in sexually selected traits is condition-dependent, but the proportion of resources invested is smaller for females in better condition (so that they remain more fecund), then plasticity might increase the mean LRS relative to that observed if females stochastically acquired breeding opportunities. To our knowledge, the circumstances where condition-dependence of female sexually selected traits elevates mean female LRS have not been formally modelled. We refer the reader to [161] for an extensive review of female ornament evolution.

Female plasticity is mainly studied by asking how it affects male-imposed costs, or how it allows a female to choose males that increase her LRS or the fitness of her offspring. We consider both. First, recent models examine in detail how plasticity affects sexually antagonistic selection [162,163]. Specifically, they ask how it affects the conflict load (fitness reduction compared with a hypothetical best-case scenario) of individuals involved in pairwise interactions, when each party controls an antagonistic trait that decreases the other party's fitness. The focus is on a situation where plasticity is unilateral, i.e. only one party shows a plastic response, while the other's strategy evolves owing to differential success of genotypes. An illustrative case in which females are the plastic party is post-copulatory sexual conflict, where males commit to a strategy by transferring seminal fluid proteins (SFPs) that females then respond to plastically. The general finding is that plasticity, compared with neither party showing plasticity, always reduces the conflict load of the non-plastic party, but that of the other party can either increase or decrease [162,163]. The intuitive reason is as follows. There are two directions in which an individual of party P (for 'plastic') might adjust its antagonistic trait p when faced with a mutant of party N (for 'non-plastic') with a slightly deviant antagonistic trait n. If p is adjusted in the same direction as the change in n (i.e. less antagonistic mutants elicit a less antagonistic response), then plasticity selects for lower antagonism in N. By contrast, if p is adjusted such that more antagonistic mutants elicit a less antagonistic response, then plasticity selects for greater antagonism in N. Thus, depending on the direction of the plastic response, plasticity × selects for either more or less antagonism in N, either increasing or reducing P's conflict load. In contrast, N's conflict load always decreases because N always evolves in the direction that elicits a less antagonistic response. This is an intriguing result, but its applicability to post-copulation sexual conflict probably depends on biological details. For example, if SFPs elevate the oviposition rate, but females can restore a nearly optimal rate with a plastic response, the evolution of more SFPs need not increase the conflict load for females. Instead, regardless of the absolute amount of SFPs transferred, the females' conflict load might reflect only the extent to which they are actually manipulated. Similarly, regardless of the absolute magnitude of a 'female resistance trait', a male's conflict load might reflect only the extent to which his mate's oviposition rate deviates from his optimum. There is no compelling reason why this deviation will necessarily be smaller when females exhibit a plastic rather than an evolved response.

Second, many studies have investigated plasticity in female mate choice. Empirical studies have shown that choice is plastically adjusted to external factors, such as the energetic costs of mate sampling, and that shifts in the threshold for acceptable mates occur based on the type and rate at which prospective males are encountered [164]. There is also good empirical evidence that female mate choice is often condition-dependent [165]. It is reasonable to assume initially that these are mainly cases of adaptive plasticity because the inherent costs of mate choice suggest that selection favours random mating if choosiness provides no benefits [49]. The genetic benefits of choosing certain males as mates are small or absent in many species [166], so adaptive mate choice implies that plasticity is likely to elevate female LRS. It should be noted, however, that while plasticity might increase female LRS in the short-term, it could favour the evolution of male traits that lower female LRS. An obvious example is that greater mean female choosiness due to plasticity selects more strongly for coercive male traits that tend to lower females' fecundity or longevity [62].

If natural selection acts similarly in both sexes there is a scenario in which condition-dependent female choice can elevate mean female LRS. The opening premise is that local adaptation is reduced when natural selection differs among populations and there is gene flow (migration). The rate of local adaptation is increased if females prefer locally adapted males, thereby reducing gene flow. In general, female mating preferences lead to local adaptation if they favour males in good condition (i.e. locally adapted) (but see [13] for complexities). This general idea was modelled by Veen & Otto [167], who developed a simple model with two patches that differ ecologically and two evolving traits: an ecological trait and a female mating preference. The strength of the preference for males in good condition was contingent on the female's ecological fit to the local patch (i.e. her condition). In this case, condition-dependent female preferences facilitate local adaptation: the costs of choice tend to slow the spread of a mating preference, but with condition dependence these costs are disproportionately borne by poorly adapted females (who are in worse condition), thereby lowering their fitness relative to that of better adapted females.

8. Do adaptive plastic responses mirror the direction of evolution?

It is tempting to assume that adaptive plasticity will produce a phenotypic shift in the same direction as selection on genotypes for fixed traits. This assumption is not universally justified. For example, Kahn *et al.* [168] modelled sex allocation decisions where mothers can re-allocate parental resources to produce more offspring when some die during the period of parental investment. They examined the effect of environmental stress that increases the mortality of sons during the period of parental investment. Although the adaptive plastic response of mothers is to produce *fewer* sons when only some mothers experience this stress, the population as a whole will evolve to produce *more* sons when the stress applies globally. This pattern arises because a locally-favoured trait (i.e. producing daughters) faces negative frequency-dependent selection at the population level, so it is not universally advantageous. Opposing directions of adaptive and evolved responses could occur in many other frequency-dependent selection scenarios.

More generally, game theory often predicts the coexistence of alternative phenotypes under negative frequency-dependent selection in a mixed evolutionarily stable strategy (ESS) [169]. A mixed ESS can manifest either as a genetic polymorphism or probabilistic expression of phenotypes (at the same frequencies as fixed phenotypes). However, if heterogeneity in local factors makes one phenotype slightly advantageous, then selection might favour a plastic response to produce the locally favoured phenotype. For example, in some spiders a mixed ESS is predicted whereby males are either monogynous (mate with one female only) or bigynous (mate with two females) [170]. If the mortality risk of mate-searching varies among males, then males with a below-average risk should plastically exhibit bigyny [171]. But, depending on the adult sex ratio, greater mortality costs of mate searching at the population level can either increase or decrease the frequency of bigyny [170]. Whether or not adaptive plastic responses match the direction of evolution of fixed differences in response to the same environmental cues depends on details that do not readily permit generalizations. However, mismatch hinges on negative frequency-dependent selection, and many adaptations are frequency-independent (e.g. temperature tolerance). If selection on a trait is frequency-independent, we suggest that it will usually be true that, following an environmental change, adaptive phenotypic plasticity and selection on mean trait values will shape phenotypes to evolve in the same direction.

9. Summary

Whether sexual selection hastens female adaptation to environmental change, and thereby reduces the likelihood of population extinction, is unresolved [5,11,13]. The extent to which male phenotypic plasticity further enhances or diminishes the effect of sexual selection is even harder to discern. We focused on female LRS rather than, as is standard in sexual selection models, mean offspring fitness. We mainly concentrated on a few ideas. First, sexual selection changes the likelihood of population extinction if it affects which males mate *and* this influences how many females breed and their mean LRS. Second, although a range of environmental cues induce plastic responses in sexually selected male traits, the condition-dependence of these traits is the factor most likely to affect female LRS in a changing environment. This is because, under such circumstances, sexually competitive males are more likely to transfer genes that elevate female LRS than to have sexually antagonistic effects. Third, condition-dependence is important when the environment changes because it can alter the strength of sexual selection, affect who mates, and change the allocation of resources to different sexually selected traits that vary in the extent to which they benefit or harm females.

We conclude that there are no general rules determining whether plasticity of sexually selected traits will reduce or elevate the risk of population extinction. This unsatisfying, but almost inevitable, conclusion concurs with inferences drawn about the effects of phenotypic plasticity on eco-evolutionary dynamics [172]. There is, however, a glimmer of hope. Recent theoretical models of sexual conflict over mating [162,163], offspring sex ratio adjustment based on sire attractiveness [60,173], and whether plastic maternal effects are more likely than plastic responses by offspring to generate adaptive outcomes [174] all show that there is the potential to make predictions about the extent to which different forms of phenotypic plasticity in sexually selected and allied traits facilitate adaptive evolution. The challenge now is to produce models that explicitly incorporate phenotypic plasticity, in order to ask questions about the role of sexual selection in facilitating population persistence in the face of rapid environmental change (see [175]).

Data accessibility. This article has no additional data.

Competing interests. We declare we have no competing interests.

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