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The Alignment of Natural and Sexual Selection

Locke Rowe[1] and Howard D. Rundle[2]

[1]Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario, Canada M5S 3B2; email: locke.rowe@utoronto.ca

[2]Department of Biology, University of Ottawa, Ottawa, Ontario, Canada K1N 6N5; email: hrundle@uottawa.ca

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Abstract

Sexual selection has the potential to decrease mean fitness in a population through an array of costs to nonsexual fitness. These costs may be offset when sexual selection favors individuals with high nonsexual fitness, causing the alignment of sexual and natural selection. We review the many laboratory experiments that have manipulated mating systems aimed at quantifying the net effects of sexual selection on mean fitness. These must be interpreted in light of population history and the diversity of ways manipulations have altered sexual interactions, sexual conflict, and sexual and natural selection. Theory and data suggest a net benefit is more likely when sexually concordant genetic variation is enhanced and that ecological context can mediate the relative importance of these different effects. Comparative studies have independently examined the consequences of sexual selection for population/species persistence. These provide little indication of a benefit, and interpreting these higher-level responses is challenging.

INTRODUCTION

Sexual selection is a consequence of variance in mating or fertilization success (sexual fitness), in contrast to natural selection, which is a consequence of variance in survival and fecundity (nonsexual fitness). Sexual selection is responsible for much of nature's diversity and some of the most extravagant traits we know, the peacock's tail being the quintessential example. At its origin, Darwin's concept of sexual selection addressed a puzzle—the evolution of exaggerated dimorphic traits that appeared to be counter to adaptation by natural selection (Darwin 1859, 1871). The supposition that sexually selected traits are often detrimental to survival has been supported by a wealth of research (Andersson 1994) and, more recently, Parker (1979) emphasized that sexually selected traits may be costly not just to the nonsexual fitness of their bearer but also to that of the opposite sex. At the same time, Darwin (1859, p. 127) argued that sexual selection may often "give its aid to ordinary selection, by assuring to the most vigorous and best adapted males the greatest number of offspring." In other words, sexual fitness may depend not just on display traits favored by the opposite sex and armaments used in same-sex competitive interactions but also on general vigor that is likewise favored by natural selection. Consequently, despite the costs of sexually selected traits, sexual selection may often be aligned with natural selection in favoring alleles of high nonsexual fitness across the genome.

Considerable research has focused on the extent to which sexual and natural selection align and whether this can offset coincident costs of sexual selection. This work has been motivated by a broader desire to understand the net consequences of sexual selection for nonsexual fitness. There is also interest in understanding how sexual selection affects specific population genetic processes that determine nonsexual fitness, including adaptation to novel environments and the purging of deleterious mutations. Experimentalists working on lab cultures have reasoned that natural selection maximizes intrinsic growth rate in these cultures and have therefore often used mean female productivity as their measure of the impact of sexual selection on fitness; if sexual selection aids natural selection, then mean individual productivity is expected to rise. These lab studies represent the bulk of relevant empirical research and are the focus of our review.

The extent to which sexual selection aids natural selection may also be relevant to the persistence of populations, and this has led to empirical studies of the relationship between sexual selection and demographic persistence. Macroevolutionists, who are interested in the extent to which within-population evolutionary processes map to higher levels of selection, have asked whether traits favored by sexual selection within populations are advantageous or disadvantageous to species persistence. With increasing anthropogenic threats to biodiversity, conservation biologists also seek to understand the properties of populations that affect risk, and sexual selection may be among these. For example, one might imagine that if sexual selection were aligned with natural selection, then it would enhance evolutionary rescue in response to anthropogenic threats such as climate change. There are challenges to this reasoning, however, which we address when considering this work.

In this synthesis, we first attempt to clarify the diversity of paths by which sexual selection can affect mean fitness. Some of these are well recognized, but others are not and are therefore often overlooked. We then consider empirical results from the laboratory, examining what these tell us about these different processes, how they may interact, and what factors may be important for mediating their impact. Finally, we turn to studies that seek to connect sexual selection to measures of population persistence.

HOW MIGHT SEXUAL SELECTION AFFECT MEAN FITNESS?

Overview

The process of sexual selection has the potential to displace traits from their natural selection optimum in both sexes, which in turn may lead to a decrease in female productivity. The potential impact of costly male traits, including exaggerated displays, has garnered the most attention, but mating biases in females, including preferences for such elaborate traits, may also be costly. Moreover, when conflict over mating is present, mating interactions themselves may reduce female productivity when harmful male traits are favored by sexual selection. The direct costs of these favored traits, mating interactions, and mating biases may be offset by indirect benefits resulting from the alignment of natural and sexual selection, but indirect effects can also be negative due to intralocus conflict. In addition, there is a distinct set of potential population effects mediated through reductions in male population size when sexually selected traits cause elevated mortality and other effects arising from the impact of sexual selection on genetic variation in fitness. We briefly describe these varied effects here and then focus on the supporting data in our review of the empirical results.

The Direct Costs of Sexually Selected Traits and Mating Biases

Sexual selection most famously displaces favored traits from their natural selection optimum, yielding costs to their bearers (Andersson 1994). In the case of male traits, any direct costs to females are mediated through a female's interactions with males. In systems where males contribute protection, resources, or care to their offspring, resources invested by males in favored traits are unavailable for investment in offspring. If there were no sexual selection, there would still be natural selection on males to invest in offspring, and males would have more to invest if freed from the costs of mate competition (Queller 1997, Kokko & Jennions 2008). In essence, as mean investment in sexually selected traits increases, male investment in offspring is expected to decrease. Consistent with this, for example, is the observation that paternal care is less common in dichromatic compared to monochromatic birds and fishes (e.g., Gonzalez-Voyer et al. 2008, Dale et al. 2015).

In contrast, when males contribute only sperm, costly male traits (e.g., bright plumage) may have no direct impact on female productivity. This situation changes, however, if there is conflict over reproduction (i.e., interlocus sexual conflict), and in these cases, costs to females are common. The most obvious costs are those associated with conflict over mating, where resistance to mating by females may favor the evolution of harmful traits in males. Examples of such traits range from persistent male courtship/harassment to genital spines and grasping traits (Arnqvist & Rowe 2005, Perry & Rowe 2015). Traits favored by male–male competition may also incidentally harm females. Examples here range from seminal proteins favored by sperm competition (Wigby & Chapman 2005) to female harm suffered during male competitive interactions (Andersson 1994). Finally, male mating biases are more widespread than originally thought and can displace favored female traits from their natural selection optima; costs here are felt directly by females (Bonduriansky 2001, Edward & Chapman 2011).

In most coevolutionary models of sexual selection, natural selection is also working on the mating bias of females (i.e., their preference). Exaggeration of this mating bias therefore comes at a cost to females, even if only in time lost to mate searching (Pomiankowski 1987, Andersson 1994). Where conflict over mating rate occurs, mating biases that come about through resistance to mating are also costly (Perry & Rowe 2015). Male mating biases are likely similarly costly to males. But, as with the costs of exaggerated traits in males, costs of male mating biases are

important to mean fitness only if transferred to females through, for example, reduced paternal investment in offspring.

It is tempting to think that female biases for male traits that reduce female productivity would be lost unless this cost is more than compensated by some other benefit from mating with those preferred males. Indeed, the so-called good-genes model of preference evolution demonstrates that the indirect benefits of mating with preferred males can offset costly mating biases (Andersson 1986, Iwasa et al. 1991, Houle & Kondrashov 2002). However, this need not be true. Consider a naturally selected sensory bias in females that, as a pleiotropic effect, favors the exaggeration of some trait in males. The favored male trait may evolve to an extent that it harms females, perhaps by inducing a costly increase in mating frequency. Consequently, there is selection in females to reduce the bias, resulting in a sensory bias that is off its natural selection optima (Arnqvist & Rowe 2005, Arnqvist 2006).

The Alignment of Natural and Sexual Selection

A distinct set of consequences of sexual selection for mean fitness center on the alignment of natural and sexual selection: Does sexual selection aid natural selection or does it impede it? Sexual selection reinforces natural selection and increases mean fitness if alleles affecting male reproductive success have pleiotropic effects on female fitness and selection acts more strongly in males than in females (Whitlock & Agrawal 2009). The alignment of natural and sexual selection is important because of its potential to increase mean fitness by reducing both drift load and mutation load (Kodric-Brown & Brown 1987, Whitlock 2000, Agrawal 2001, Whitlock & Agrawal 2009) and by increasing the degree and rate of adaptation to local environments (Whitlock 2000, Proulx 2002, Lorch et al. 2003, Candolin & Heuschele 2008). Alignment is argued to be common because mating interactions typically favor vigorous, high-condition individuals, and most genes likely contribute to condition (Andersson 1986, Rowe & Houle 1996, Whitlock & Agrawal 2009). Consistent with an indirect benefit of sexual selection is the often-observed correlation between mating success in males and nonsexual fitness in both sexes, which is best known as the basis of the good-genes model of preference evolution (Kirkpatrick & Ryan 1991, Andersson 1994). However, alignment is not limited to female preference evolution; it can arise from any form of mate competition that favors high-condition individuals. For example, the outcome of male–male competitive interactions may be condition dependent (Andersson 1994), and male mating preferences often appear to favor high-fecundity females (Bonduriansky 2001, Edward & Chapman 2011). Also consistent with alignment, studies indicate that new mutations tend to be harmful in both sexes and affect males more than females (Mallet et al. 2011, Mallet & Chippindale 2011, Sharp & Agrawal 2013, Grieshop et al. 2016).

Working against alignment is intralocus conflict, which results from sexually antagonistic selection on the largely shared genome of the sexes (Lande 1980, Bonduriansky & Chenoweth 2009). Given this shared genome, the intersexual genetic correlation for most traits is expected to be strong and positive, and data support this (Poissant et al. 2010, Griffin et al. 2013). When sexual selection displaces traits from their natural selection optima in one sex, it has a similar effect in the other sex, conditioned on the strength of the intersex genetic correlation. If it is common that traits exaggerated by sexual selection in males are consequently exaggerated to an extent in females, then costs to female productivity are expected to be common. In effect, an attractive father tends to produce daughters that are less fit (e.g., Chippindale et al. 2001). Yet, the widespread occurrence of sexual dimorphism suggests that intralocus conflict may be transitory, with mechanisms such as sex-biased gene expression allowing the sexes to reach their sex-specific optima.

The extent to which intralocus conflicts are resolved is currently an open topic (Kasimatis et al. 2017, Mank 2017, Rowe et al. 2018).

Demographic Effects of Exaggerated Traits

The costs of male sexually selected traits may be great enough to significantly affect the population sex ratio, which in turn may have both negative and positive effects on female productivity. Male mortality may be sufficiently high that some females go unmated, even in polyandrous systems. Kokko & Brooks (2003) argue that this is possible in rapidly fluctuating populations but unlikely to be common in stable populations. In the latter, a mating bias that favors the mortality-inducing trait should be disfavored if it comes with the extreme cost of a risk of zero fecundity (Kokko & Brooks 2003; but see Houle & Kondrashov 2002). On one hand, in systems with paternal care, an increase in male relative to female mortality decreases the total pool of male care and therefore may decrease mean female fecundity. On the other hand, a reduction in the number of males in a population may free up resources for females and therefore increase mean productivity (Kokko & Brooks 2003, Agrawal & Whitlock 2012). There is growing evidence that intersexual resource competition may be more common than initially thought (De Lisle 2019), suggesting that male-biased mortality could benefit female productivity.

Effects of Sexual Selection on Variance in Fitness

A final set of consequences arise at the population level from changes in the genetic variance for fitness. One such factor concerns sexual selection's effect on genetic drift. Sexual selection increases the variance in male fitness through reproductive skew, and increased variance in male fitness (above the ideal Poisson expectation) reduces the effective population size, N_e (Crow & Kimura 1970). This, in turn, causes a genome-wide increase in the strength of drift that may offset the benefit of sexual selection arising through strengthened selection in males (A Singh & AF Agrawal, manuscript in review). However, recent theory and empirical results suggest that the effect of sexual selection on N_e is small if the total variance in fitness has a large stochastic component (Pischedda et al. 2015; A Singh & AF Agrawal, manuscript in review), for instance, in high-fecundity taxa in which random juvenile mortality is important (as is typical of many lab systems).

Genetic variance in fitness may also be affected by targeted male harm. In systems where conflict has favored harmful male traits, if males prefer intrinsically high-fecundity females (i.e., those of high genetic quality), then these females experience disproportionate male harm (i.e., a cost of attractiveness) (Long et al. 2009). This nonrandom allocation of male harm reduces the variance in fitness among females, decreasing or even eliminating the selective advantage of any beneficial genetic variants underlying high genetic quality in females. The result is a reduced efficacy of natural selection, in addition to the direct cost of male harm that females experience. The reverse may occur if high-quality females are more resistant to male harm. Here, male harm can increase the efficiency of natural selection.

Effects on fitness variation can also arise from assortative mating (or fertilization) by fitness. For example, if mating biases are condition dependent, or if male–male competition is more intense over high- than low-quality females, then a positive genetic correlation can arise in the fitness of mates (Sharp & Agrawal 2009). Positive assortative mating by genetic quality increases the genetic variance in fitness among offspring in the population, increasing the efficiency of natural selection (Fisher 1919, Rice 1998). Theory suggests that, when costly, mate competition generates a positive genetic correlation in the fitness of mates (Fawcett & Johnstone 2003), and the prevalence of size assortative mating (e.g., Janicke et al. 2019) suggests that positive assortative mating by fitness could be common. However, a negative correlation in the fitness of mates could also arise from

sexual selection, for example, if high-quality males are particularly successful at mating low-quality females (Sharp & Whitlock 2019). Such disassortative mating would decrease the genetic variance in fitness among offspring, thus decreasing the efficacy of natural selection.

Finally, mutation is the ultimate source of genetic variation, and sexual selection may affect this as well. Postcopulatory sexual selection on sperm competitive traits often leads to greater sperm production, and the resulting increase in germ-line cell divisions, compared to that during egg production in females, may increase the mutation rate in males (Ellegren 2007). Under some conditions, this may increase mutation load, but evidence here is lacking (Whitlock & Agrawal 2009).

In summary, the outcomes of sexual selection, including favored traits, mating interactions, and mating biases themselves, can have substantial effects on mean fitness. Most appear to be negative, often because of a misalignment between natural and sexual selection. However, the condition dependence of mating biases, and especially favored traits, may offset these costs by aligning natural and sexual selection. In these cases, sexual selection aids natural selection in increasing nonsexual fitness. The net effect of these varied effects is not predictable without knowing the extent to which each is playing a role in a given study system or lineage, past and present. Perhaps as a result of this, a great deal of effort has been expended to understand these various contributions in experimental systems and their dependence on local conditions and population history. In the next section, we synthesize the results of these experimental studies and point to both obstacles that remain and lessons learned.

EXPERIMENTAL MANIPULATIONS OF MATING SYSTEMS

Lab studies have given particular attention to testing the fitness consequences of sexual selection. One common experimental approach, pioneered by Partridge (1980), is particularly relevant to the effect of sexual selection on mean fitness. The approach involves altering the opportunity for sexual selection by manipulating mating systems and then, after one or more generations, comparing the response with some estimate of mean fitness. Sexual selection is largely eliminated in one treatment by enforcing monogamy via the random pairing of individuals, whereas sexual selection is allowed in the other treatment via some form of polygamy or polyandry. These studies were originally motivated by a desire to understand the genetic consequences of mate choice (i.e., testing for indirect benefits). As the field developed, costs of intra- and intersexual conflict were identified, and attention shifted to whether indirect benefits could offset these costs (e.g., Holland & Rice 1999, Holland 2002). Other experimental studies began addressing more specific questions, in some cases employing modified experimental designs to target a particular process, for example, testing whether sexual selection can help purge deleterious mutations, decrease mutation load, or increase the rate of adaptation.

As a body of work, results from experimental manipulations of mating systems are mixed and sometimes complex, with some suggesting a net benefit of sexual selection (e.g., Partridge 1980, Promislow et al. 1998, Radwan 2004, Hollis et al. 2009, Jarzebowska & Radwan 2010, Almbro & Simmons 2013, Lumley et al. 2015, Gibson Vega et al. 2020) and others not (e.g., Holland 2002, Hollis & Houle 2011, Arbuthnott & Rundle 2012, Chenoweth et al. 2015). A recent meta-analysis of 65 experiments that compared some aspect of nonsexual fitness between mating treatments found that sexual selection tended to be beneficial, although results were highly variable and the average effect was weaker for measures more closely linked to lifetime reproductive success (Cally et al. 2019). Many of these studies quantified only one or a few components of fitness, and because these can trade off, they are hard to interpret with respect to the net effect of sexual selection. Nevertheless, given the many potential costs, it is perhaps not surprising that a net benefit of sexual selection may be weak, and sometimes absent, and that results are heterogeneous, given that effects

may vary in importance among systems. For example, in taxa or experimental conditions with little conflict, a net benefit of alignment may be more likely. Here, we highlight several insights that emerge from considering this large body of work.

Mating Treatments Can Affect Much More Than Indirect Benefits

A manipulation of mating systems alters the opportunity for the indirect benefits that may result from the alignment of sexual and natural selection, but it can also alter many of the other effects of sexual selection described earlier (see the section titled How Might Sexual Selection Affect Mean Fitness?). These effects are sometimes ignored, but populations may evolve in response to them, and differences in fitness between mating treatments must therefore be interpreted in light of them. For example, the reproductive interests of males and females coincide under monogamy, eliminating interlocus conflict, and fitness may therefore increase in response. For example, Holland & Rice (1999) demonstrated that monogamous *Drosophila melanogaster* populations evolved males that were less harmful, females that were less resistant to male harm, and a greater net reproductive rate compared to polygamous populations. Sexual selection is also a common source of sexually antagonistic selection, so its removal under monogamy is likely to decrease intralocus conflict, allowing female phenotypes to evolve closer to their natural selection optima, hence increasing female fitness. This may also have contributed to the results of Holland & Rice (1999). The importance of altered conflict between mating treatments in affecting mean fitness depends, in part, on the prevalence of intra- and interlocus conflict in the focal population, which is likely to vary among systems. *D. melanogaster* is a workhorse of studies manipulating mating systems, and evidence from lab populations suggests strong interlocus sexual conflict (Fowler & Partridge 1989, Rice et al. 2006, Hollis et al. 2019) and substantial unresolved intralocus conflict (Chippindale et al. 2001, Pischedda & Chippindale 2006, Prasad et al. 2007, Ruzicka et al. 2019). All else being equal, effects of mating treatments on gender load may overwhelm those on alignment under such conditions, as shown by Holland & Rice (1999).

Targeted male harm is also greatly reduced or eliminated under experimentally imposed random mating (i.e., monogamy), so its presence in polygamy may weaken natural selection and hence offset any indirect benefits of sexual selection. Targeted male harm was implicated in three recent mating system manipulations that failed to find a benefit of polygamy for either adaptation or purging in *Drosophila serrata* and *D. melanogaster* (Arbuthnott & Rundle 2012; Chenoweth et al. 2015; Yun et al. 2017, 2018). Although we lack direct tests in other species, male mate preferences are widespread and often target high-fecundity females (Amundsen & Forsgren 2001, Bondurianstiky 2001), and male harm is common (Arnqvist & Rowe 2005), providing the necessary conditions for targeted male harm. As noted in the section titled Effects of Sexual Selection on Variance in Fitness, differential resistance by females could reverse this effect by increasing genetic variance in female fitness, thus strengthening natural selection. Condition dependence of female resistance has received little attention (Rostant et al. 2020), although condition-dependent mate preferences are known (Cotton et al. 2006), and differential female resistance was recently implicated in an observed benefit of a polygamy treatment in *D. melanogaster* (MacPherson et al. 2018).

Finally, assortative mating by fitness can occur under polygamy but is likely to be absent under monogamy, causing the efficiency of natural selection to differ between mating treatments. There are few direct tests for assortative mating by fitness, all in *D. melanogaster*, and results are mixed but generally negative (Sharp & Agrawal 2009, Sharp & Whitlock 2019). Whether and how mating treatments affect fitness through changes in assortative mating is thus unclear at this time.

Our analysis in this section suggests that the indirect benefits resulting from the alignment of natural and sexual selection may be unlikely to overcome the costs of sexual selection in systems dominated by sexual conflict. But benefits of polygamy have been observed in a number of studies

manipulating mating systems (Cally et al. 2019), suggesting costs arising from conflict do not always overwhelm the benefits of sexual selection. What might explain this variation among studies?

Alignment Depends on the Nature of Genetic Variation in Fitness

The amount and type of segregating genetic variation are central for the response to selection. In natural populations, deleterious alleles with sexually concordant fitness effects are continually introduced not only by mutation but also via maladaptive gene flow from neighboring populations and due to local environmental change causing previously beneficial alleles to become deleterious. When genetic variation is dominated by alleles with sexually concordant effects, alignment is more likely because males of high reproductive fitness sire both sons and daughters with high fitness. In contrast, in populations that are well adapted to a stable environment, purifying selection may erode sexually concordant variation, which may instead be dominated by a relatively small number of sexually antagonistic alleles segregating at intermediate frequencies (Connallon & Clark 2012, 2014). In this case, high-fitness males tend to sire low-fitness daughters such that natural and sexual selection are not aligned. Lab populations may be extreme examples of the latter given the unusual stability of their environments and general absence of gene flow, resulting in populations residing closer to a peak than natural populations (Long et al. 2012).

Insight into how the nature of genetic variance may affect results can be gained from studies that have altered it and then assayed the consequences. There are several ways to do this, and these fall into two broad categories. First, populations can be displaced from their adaptive peak by changing their environment or via artificial selection, both of which are expected to increase the availability of sexually concordant fitness variation. Second, novel genetic variants can be introduced into a population, circumventing issues of how evolutionary history has shaped standing genetic variance. For example, maladaptive alleles can be introduced by crossing populations adapted to different environments, via mutagenesis, or by relaxing natural selection to let deleterious mutations accumulate on their own. Individual alleles, beneficial or deleterious, can also be backcrossed into populations.

What have we learned from such studies? Results are again mixed, although several are consistent with a benefit of polygamy (e.g., Radwan 2004, Fricke & Arnqvist 2007, Hollis et al. 2009, Jarzebowska & Radwan 2010, McGuigan et al. 2011, Long et al. 2012, Plesnar-Bielak et al. 2012, Jacomb et al. 2016, Gibson Vega et al. 2020). This suggests that indirect benefits are more likely to overcome the various costs of sexual selection in so-called off-peak populations, in which sexually antagonistic variation is less predominate. A few of these studies that included on-peak comparators are consistent with this. For example, Fricke & Arnqvist (2007) and Plesnar-Bielak et al. (2012) demonstrated benefits of polygamy in a novel but not ancestral environment in seed beetles and bulb mites, respectively (see also Parrett & Knell 2018). Long et al. (2012) also showed that attractive males tended to sire high-fitness sons (and daughters) in off-peak populations harboring maladaptive variation due to gene flow, but they sired low-fitness sons in on-peak populations (i.e., those in which gene flow was absent). Nevertheless, some studies have found no benefit of polygamy in off-peak populations (e.g., Holland 2002, Radwan et al. 2004, Rundle et al. 2006, Hollis & Houle 2011, Plesnar et al. 2011, Power & Holman 2015) or when tracking frequency of individual genetic variants (Arbuthnott & Rundle 2012). Such mixed results suggest there are other effects of mating treatments and/or variation in other key factors such as local ecological conditions.

Ecology Matters

It is well established from studies of natural populations that ecological context mediates natural selection on mating biases and favored traits; this context can therefore affect sexual selection

and conflict and hence their outcomes (Emlen & Oring 1977, Rowe et al. 1994, Candolin & Heuschele 2008, Fricke et al. 2009; see also Arbuthnott et al. 2014 for laboratory studies). Until recently, little attention had been given to ecological factors that may mediate sexual selection's impact on mean fitness in lab studies. Most experiments manipulating mating systems have used small and highly simplified environments. However, three recent *Drosophila* studies demonstrated more rapid adaptation and purging under polygamy when mating occurred in environments that were larger and/or slightly more structurally complex (Colpitts et al. 2017, Singh et al. 2017, Yun et al. 2018). There are several nonmutually exclusive reasons why the environment may matter in this way.

First, mating environments may affect the expression and evolution of male harm. In larger, more complex environments, females may have more control over sexual interactions because they can avoid males and escape unwanted sexual attention, lowering mating rates. Males may therefore be less able to express harm, and interlocus conflict may be reduced, favoring the evolution of decreased harmfulness. Costs of interlocus conflict and targeted male harm may thus be reduced in complex compared to simple environments, making it easier for alignment to overcome these. Mechanistic studies indicate that this underlies, at least in part, the results of the experiments above that demonstrated a benefit of polygamy in complex mating environments. Yun et al. (2017, 2019) showed that, in the complex compared to simple mating environments, sexual interactions were less frequent, mating rates were lower, the expression of male harm was reduced, and targeted male harm was eliminated. Female resistance to male harm was also more condition dependent in the complex environment, strengthening natural selection on female quality (MacPherson et al. 2018). Males in the complex environment also evolved to become less harmful (Yun et al. 2019).

Second, mating environments may also contribute to the alignment of sexual and natural selection by altering the condition dependence of male reproductive success. In a highly simplified environment, the reproductive advantage of healthier, more vigorous males may be reduced because some components of sexual fitness are less relevant (e.g., territoriality, search effort, female choice). Weakened sexual selection on condition would decrease the benefit of alignment. Little attention has been given to this, although selection against deleterious phenotypic marker mutations was stronger on average in a larger environment in which males had to search for females (MacLellan et al. 2009). Finally, positive assortative mating by fitness may be more likely in larger, more complex mating environments. *D. melanogaster* is the only species in which direct tests for assortative mating by fitness have been performed, and these find little evidence for it (Sharp & Agrawal 2009, Sharp & Whitlock 2019), but environmental effects on assortative mating have received little attention. Results such as these provide compelling evidence that ecology matters and suggest that it may have predictable effects on the consequences of sexual selection for nonsexual fitness. However, that a relatively minor alteration of laboratory environments causes a dramatic change in the net effect of sexual selection is also concerning.

POPULATION PERSISTENCE AND EXTINCTION

Experimentalists have largely been interested in understanding the processes of sexual selection and how they affect the nonsexual fitness of males and females. In contrast, other more macrolevel studies have focused on the consequences of sexual selection for population persistence. The fact that sexual selection can affect female productivity suggests that it may affect population persistence as well, and this is inherently interesting to macroevolutionists and conservation biologists. However, understanding the effects of sexual selection on lineage extinction and population persistence seems a particularly challenging endeavor, even in the best-known systems. First, such studies necessarily take a comparative approach in which it is difficult to estimate differences in sexual selection among groups, past and present. For example, the strength of sexual selection is

typically inferred from some measure of dimorphism, but dimorphism may reflect differing natural selection and may fail to capture a signal of postcopulatory sexual selection. Second, there are diverse ways by which sexual selection can affect mean fitness, as discussed extensively in the section titled How Might Sexual Selection Affect Mean Fitness, and the relative importance of these varies among species (e.g., due to differences in the extent of conflict) and may also differ systematically between the lab and the field (e.g., demographic costs are often reduced or eliminated in the former).

Finally, and perhaps most importantly, the link between the response to selection within populations and population persistence is complex and contingent. For selection within populations to improve persistence, there must be a coupling of relative and absolute fitness (Haldane 1932). This coupling exists under simplified conditions in which interactions among individuals, either directly or mediated through the environment, have negligible fitness consequences. In this case, selection maximizes mean fitness (Lande et al. 2017) and therefore should benefit persistence. While these conditions may be approximated in some lab cultures, they seem unlikely to be common in nature (Metz et al. 2008, Ferriere & Legendre 2018). A well-known example of decoupling is the tragedy of the commons whereby selection for increasing consumption of a limited resource may drive the population to a Darwinian extinction (Hardin 1968, Webb 2003). We have already discussed some cases where sexual interactions themselves deviate from these simplified conditions. For example, male mating harassment, favored by sexual selection on males, may reduce female productivity. Theory has analogized this process to a tragedy of the commons, demonstrating that it may lead to extinction (Rankin et al. 2011, Svensson & Connallon 2019), and there is empirical support for such a dynamic in lizards under seminatural conditions (Le Galliard et al. 2005). Houle & Kondrashov's (2002) model of the good-genes process is another example where female preferences, which favor high-genetic-quality males, can under some conditions lead to such costly exaggeration of male traits that populations go extinct. With these perhaps-daunting obstacles in mind, we briefly review studies that have attempted to assess the relationship between population persistence and sexual selection.

In a recent study of cytheroid ostracods, extinction as a function of sexual dimorphism in shell shape and size was estimated from the fossil record of preserved carapaces (Martins et al. 2018). In extant species, increasing male reproductive investment in the copulatory apparatus leads to an elongation of the male carapace. Results suggest that, during the Late Cretaceous period, the most dimorphic species had a tenfold increase in extinction rate compared to the least. A striking feature of the group is a tendency toward female-biased adult sex ratios (Martins 2019), suggesting that reproductive investment in males may come at a survival cost, and this is supported by the observation that female bias is an increasing function of shape dimorphism (Hunt et al. 2017). Little is known of the mating system in this group, including whether mating interactions are costly to females, and therefore, a suite of potential causes for this evolutionary pattern are difficult to infer. However, the results are compatible with a demographic effect whereby a general shortage of males and reduced N_e makes these populations vulnerable to collapse when environmental change leads to population decline. This view is supported by recent analyses demonstrating a loss of the most dimorphic groups following the Cretaceous–Paleogene mass extinction (Martins et al. 2020).

In the absence of fossil data in which the sexes can be distinguished, historical extinction can be inferred from extant species and a phylogenetic hypothesis (e.g., Svensson & Waller 2013, De Lisle & Rowe 2015). However, recent analyses demonstrate that we can have little confidence in methods that aim to distinguish extinction from reduced speciation (Louca & Pennell 2020). This leaves just three approaches: direct observations of extinction or local population persistence in the wild, estimates of extinction risk, and laboratory experiments. In an example of the first

approach, Doherty et al. (2003) used 21 years of data from the North American Breeding Bird Survey to estimate the impact of dichromatism on population persistence for several hundred bird species. These analyses indicated a 23% reduction in local year-over-year persistence in dichromatic versus monochromatic species but no impact on species number due to higher turnover in dichromatic species. While these results have important implications for conservation and metapopulation dynamics, it is difficult to know what they mean for our understanding of sexual selection and extinction.

A number of studies have examined the impact of plumage dimorphism on the success of island introductions of birds (McLain et al. 1995, 1999; Sorci et al. 1998; Donze et al. 2004). The results here are mixed, with early studies, focused on passerines, indicating that dimorphic species are considerably less likely to establish, while larger, more recent studies tend toward no impact. For example, in a study of 132 passerine species introduced to nine oceanic islands, McLain et al. (1999) found that species with dimorphic plumage were less likely to survive introduction. More recently, in a large study involving over 2,000 introductions of birds, mammals, and fish, little or no impact of dimorphism in ornaments was found, with only a small negative effect of size dimorphism on the introduction success of mammals (Jeschke & Strayer 2006). These introduction studies may best be viewed as assessments of the impact of sexual selection on the ability of species to colonize a new patch, at a small population size, and therefore may not be directly comparable to the other natural population-based studies. The small population size means that they are particularly susceptible to demographic stochasticity and Allee effects, and this may be exacerbated in sexually selected populations because both mating skew and any mortality costs of sexually selected traits reduce male numbers (Kokko & Brooks 2003, Martínez-Ruiz & Knell 2017). Studies have consistently demonstrated that the population size of introduced birds is a strong predictor of introduction success (Duncan et al. 2014, Redding et al. 2019). These studies have also demonstrated strong effects of local conditions on introduction success, making any potential effects of dimorphism more difficult to detect.

Examples of the second approach include a number of studies that have estimated the effects of sexual selection on current extinction risk, using either the International Union for Conservation of Nature (IUCN) system for ranking species' extinction risk or direct measures of population decline. In an early study of ~1,000 bird species, Morrow & Pitcher (2003) assessed the relationship between three indices of sexual selection (size dimorphism, dichromatism, and relative testes size) and IUCN extinction risk. Of the three metrics, only increased testes size was related to extinction risk. In similar studies of mammals, neither size dimorphism nor testes size was related to extinction risk in one study (Morrow & Fricke 2004), but a relationship between risk and increasing horn dimorphism, but not size dimorphism, was reported in bovids (Bro-Jørgensen 2014). In amphibia, extinction risk decreases with size dimorphism, but in this group size dimorphism is thought to be largely driven by natural selection on females (De Lisle & Rowe 2015). The IUCN system is primarily based on demographic factors that are believed to be associated with increased risk, specifically small population sizes and ranges and temporal declines in both (Mace et al. 2008). One advantage is that it provides a consistent index of risk, but it is limited in species coverage and may be biased by anthropogenic factors that play a lesser role in longer term patterns of extinction. Other measures have been used that capture similar current threats to populations, which are also likely to be dominated by anthropogenic factors. For example, Prinzing et al. (2002) found no effect of plumage or size dimorphism on recent (1970–1995) trends in population size of non-passerine birds of Central Europe. In contrast, Parrett et al. (2019) quantified horn dimorphism in beetles in Malaysian Borneo, documenting a greater loss of monomorphic than dimorphic species in response to recent habitat alterations but also a negative association of relative testes size with persistence.

Overall, these studies of population persistence and extinction do not indicate a consistent impact of sexual selection, though most were either negative or null, suggesting no advantage to sexual selection. Where multiple indices of sexual selection were used, associations with persistence were not consistent. This should make us wary about indices of sexual selection. This variation among indices may result from a range of factors, one being differences among traits in their power to detect effects, another being trade-offs among sexually selected traits (Parrett et al. 2019). However, there is also the possibility that the evolution of some sex differences is more related to natural than sexual selection. This is most likely in traits that are closely related to resource use, such as size (e.g., Schoener 1978, De Lisle 2019), and sexual size dimorphism is a commonly used index of past sexual selection. With some exceptions, these field studies also focus on recent population trends in often abruptly altered habitats, in some cases on very small populations. All of these factors put an extra emphasis on any impacts of sexual selection on demographic parameters, which may affect susceptibility to demographic stochasticity (Lande 1988, 1993). The study of extinction in ostracods by Martins et al. (2018) is an exception because of its historical nature. But here, too, there is a suggestion that sexual selection's effect on male population size may play a role, given the highly female-biased sex ratio in the group.

Turning to the third approach, only a few lab experiments that manipulated mating systems have included measures of population persistence. In some, the design did not allow cumulative population declines, instead using persistence as a means of assessing mutation load (e.g., McGuigan et al. 2011, Lumley et al. 2015). However, four other experiments were more analogous to the macrolevel studies where cumulative population declines were permitted. These studies used small populations (Jarzebowska & Radwan 2010, Plesnar-Bielak et al. 2012, Godwin et al. 2020), or populations became small as environmental stress increased (Parrett & Knell 2018). Drift increases the contribution of deleterious recessive alleles to fitness in such populations, increasing the availability of sexually concordant variation. In three cases, populations were also maintained in novel or continually changing environments (Plesnar-Bielak et al. 2012, Parrett & Knell 2018, Godwin et al. 2020), likely further enhancing sexually concordant variation. In contrast to the field results above, where null or negative effects of sexual selection predominate, these studies found positive effects of polygamy on persistence. An exception is Parrett & Knell (2018), who found benefits of polygamy for fitness but no impact on persistence. However, the number of replicate populations was modest (four per treatment), so power may have been low. Collectively, the results of these studies are consistent with other laboratory studies in that sexual selection is more likely to have a positive impact in off-peak populations. Polygamy was shown to benefit fitness components (e.g., female fecundity) in these or other experiments in these systems (e.g., Radwan 2004, Lumley et al. 2015; but see Radwan et al. 2004, Plesnar et al. 2011), suggesting a coupling of relative and absolute fitness in these cases and hence the opportunity for sexual selection to benefit persistence. The authors argue that sexual selection under polygamy reduced the likelihood of an extinction vortex due to declining fecundity (Plesnar-Bielak et al. 2012, Godwin et al. 2020). However, the small population sizes used in these studies may also allow demographic factors to contribute. For instance, in the face of rising male sterility, multiple mating by females under polygamy may have provided reproductive assurance by ensuring sufficient sperm (Plesnar-Bielak et al. 2012).

CONCLUSIONS

The potential effects of sexual selection on nonsexual fitness are numerous and often conflicting. The process of sexual selection has the potential to displace phenotypes in both sexes from their natural selection optima, including mating biases, preferred traits, and mating interactions

themselves. Moreover, the largely shared genome of the sexes means that traits in one sex may be displaced from their optima due to selection in the other sex. Each of these has negative effects on mean fitness if it affects female fitness directly or if it affects females through their interactions with males. At the same time, sexual selection may give aid to natural selection when better adapted, more vigorous males have greater reproductive success. Additionally, mating skew and assortative mating can also affect the nature of standing genetic variance in the population, with both positive and negative consequences for mean fitness.

Laboratory studies have confirmed that each of these potential effects occurs under some conditions in some model organisms. These studies have also shown us that the net effects on mean fitness, that is, the extent to which the myriad potential costs are offset by the indirect benefits accrued through the alignment of natural and sexual selection, can be sensitive to the mating system (e.g., low versus high conflict), the mating environment employed in the lab, and the nature of genetic variation in the population. Indirect benefits appear common, particularly in populations that have been displaced from their adaptive peak and those that have been tested in more heterogeneous environments. Natural populations, living in variable environments and with maladaptive gene flow from neighbors adapted to differing local conditions, may benefit more from sexual selection than is typically seen in the more isolated and uniform environment of model laboratory systems. However, laboratory studies can contribute to evaluating these ideas, given that environments and genetic variation can be manipulated. Going forward, controlled studies, with varied treatment levels, will be most informative, as many past studies lack controls or comparators, instead altering some factor consistently across all replicates. Limited attention has been given to the importance of ecology and the nature of genetic variation, but a few recent studies suggest these may be key. Additionally, many experiments evaluate components of lifetime reproductive success, yet these can trade off, and the extent to which selection maximizes lifetime reproductive success is not addressed, complicating inferences concerning alignment and the net effects on population mean fitness.

There are too few studies examining the association between sexual selection and population persistence, extinction risk, and extinction itself to draw any conclusions about pattern. The results here tend to be null or negative, which may be viewed as a surprise because a large fraction of them use metrics (e.g., IUCN rankings) that would seem particularly sensitive to recent environmental change, which is exactly where we expect to see some benefits through the alignment of natural and sexual selection. Some of these populations are small (e.g., island introductions), such that demographic stochasticity may be exacerbated by a reduction in male numbers or their contributions to offspring, which may result from costly favored traits. But perhaps we should not be surprised; it is only under very specific conditions that we expect natural selection to maximize population persistence. When such conditions are not met, the alignment of sexual and natural selection may increase or decrease population persistence. This uncertainty, together with the challenges of inferring sexual selection from indices of dimorphism, makes us skeptical about predicting or observing any association between sexual selection and population persistence.

The essence of the problem with translating the impact of natural selection, and by extension the alignment of sexual and natural selection, to population persistence is that relative and absolute fitness may often be uncoupled (Haldane 1932, Webb 2003, Ferriere & Legendre 2018). We have discussed the uncertainties this introduces to studies of population persistence. However, it is also a concern for the design of lab experiments. Many lab studies that conclude that sexual selection is aligned with natural selection have done so by demonstrating that sexual selection increases mean fitness (e.g., female productivity) beyond that attained through natural selection alone. This inference rests on the assumption that natural selection itself maximizes mean absolute fitness, which is valid only under very specific conditions. For example, the intrinsic rate of reproduction may

not be maximized by natural selection when there is density-dependent selection (Charlesworth 1994), and some lab cultures include density dependence. This suggests a need for more care in the design of lab studies and caution in their interpretation.

In summary, we have learned a lot about how the process of sexual selection can affect mean fitness in the lab and how the nature of populations and their local environments mediate these effects. Results from these lab studies have done much to confirm the varied evolutionary processes and outcomes that can arise from sexual selection, how they may interact, and how they may influence mean fitness. Moreover, answers to longstanding questions, such as when we might expect a good-genes process versus an interlocus-conflict process to dominate, are within reach. We know a lot less about the impact of sexual selection on population persistence and extinction, and we are not optimistic that there will be a consistent answer. A central message from both lab studies and theory is that we should not expect sexual selection's impact on mean fitness to be consistent among species, or even within species.

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Contents

Errata

An online log of corrections to *Annual Review of Ecology, Evolution, and Systematics* articles may be found at http://www.annualreviews.org/errata/ecolsys