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Report

The Effect of Sexual Selection on Offspring Fitness Depends on the Nature of Genetic Variation

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Summary

Whether the changes brought about by sexual selection are, on the whole, congruent or incongruent with the changes favored by natural selection is a fundamentally important question in evolutionary biology. Although a number of theoretical models have assumed that sexual selection reinforces natural selection [1, 2], others assume these forces are in opposition [3–5]. Empirical results have been mixed (see reviews in [1, 6–8]) and the reasons for the differences among studies are unclear. Variable outcomes are expected if populations differ in their evolutionary histories and therefore harbor different amounts and types of segregating genetic variation. Here, we constructed populations of *Drosophila melanogaster* that differed in this regard to directly test this hypothesis. In well-adapted populations, sexually successful males sired unfit daughters, indicating sexual and natural selection are in conflict. However, in populations containing an influx of maladaptive alleles, attractive males sired offspring of high fitness, suggesting that sexual selection reinforces natural selection. Taken together, these results emphasize the importance of evolutionary history on the outcome of sexual selection. Consequently, studies based on laboratory populations, cultured for prolonged periods under homogeneous conditions, may provide a skewed perspective on the relationship between sexual and natural selection.

Results

We compared the effects of sexual selection on fitness in replicate populations close to their adaptive peaks (“peak populations”) and in populations pushed off their peak by an influx of migrant alleles (“off-peak populations”). Our peak populations, consisted of three replicate populations of *Drosophila melanogaster* that were well-adapted to cadmium-containing media, whereas our off-peak populations consisted of three replicate F2 populations created by crossing each of the cadmium-adapted populations with populations adapted to ethanol-containing media. These experimental populations are meant to bracket the range of possibilities of natural populations, some of which will have largely fixed adaptive variants, whereas in others such variants segregate at intermediate frequency. In each population, we identified sexually successful and sexually unsuccessful males, and used them to sire offspring that were raised in a competitive environment and assayed for viability, development and fitness (see Supplemental Experimental Procedures available online).

Our key prediction was that sexually successful males in off-peak populations would sire fitter offspring of both sexes, however, in peak populations, such males may sire unfit daughters because sexually antagonistic alleles are expected to make a relatively greater contribution to the genetic variance in fitness. Our analysis of daughter fitness revealed a significant interaction effect between evolutionary history and sire success status (likelihood ratio test: $\chi^2 = 33.9$, df = 1, $p < 0.0001$). This indicates that the difference in fitness between daughters sired by successful and unsuccessful males varies between peak and off-peak populations. In fact, the data show that the genetic consequences of being sired by a successful male differs in sign between populations of different evolutionary histories (Figure 1). In off-peak populations, daughters sired by successful males were significantly more fit than those sired by unsuccessful males ($\chi^2 = 27.1$, df = 1, $p < 0.0001$). In contrast, the daughters sired by successful males in peak populations were significantly less fit than those sired by unsuccessful males ($\chi^2 = 8.0$, df = 1, $p = 0.0046$). These results are consistent with the hypothesis that sexually antagonistic variation dominates in our peak populations but sexually congruent variation dominates in our off-peak populations.

In both peak and off-peak populations, we expected successful males to sire successful sons, though we predicted the effect to be larger in off-peak populations simply because of the additional abundance of “good genes” type variation. Consistent with this, we found that evolutionary history affected the genetic benefits to sons (Figure 2). Specifically, there was a significant interaction between evolutionary history and sire success status in the analysis of son fitness similar to that seen in the analysis of daughter fitness ($\chi^2 = 5.9$, df = 1, $p = 0.0151$). In the off-peak populations, sons sired by successful males were significantly more fit than those sired by unsuccessful males ($\chi^2 = 14.3$, df = 1, $p = 0.0002$). Unexpectedly, there were no significant differences in the reproductive success of sons of successful versus unsuccessful males in any of the peak populations ($\chi^2 = 0.49$, df = 1, $p = 0.48$).

In addition to measuring adult fitness components, we measured juvenile survivorship among the offspring of successful and unsuccessful males. There was no significant effect of population history, sire success status, or their interaction on egg-to-adult survivorship (see Supplemental Results). We also measured development time and found no significant interaction between evolutionary history and sire success status (see Supplemental Results). We did find a significant effect of history on development time with both sons and daughters in peak populations developing more quickly than those from off-peak populations (sons: $\chi^2 = 11.0$, df = 1, $p = 0.0009$; daughters: $\chi^2 = 8.6$, df = 1, $p = 0.0034$). We found an even smaller, though still significant, effect of sire success status on both son and daughter development times (sons: $\chi^2 = 56.0$, df = 1, $p < 0.0001$; daughters: $\chi^2 = 45.5$, df = 1, $p < 0.0001$) with successful sires producing more slowly developing offspring.

Discussion

Over a century and a half after sexual selection was first conceptualized [9], it still remains unclear whether sexually

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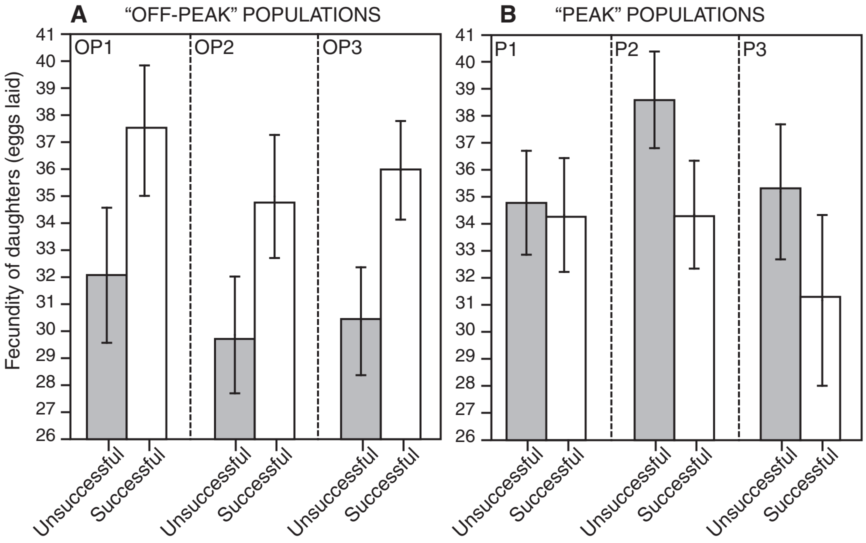

Figure 1. Effects of Sexual Selection and Evolutionary History on the Fitness of Female Offspring

Mean fitness of *D. melanogaster* daughters sired by sexually "unsuccessful" and "successful" males in three replicate off-peak (A) and peak (B) populations, estimated from the statistical model. Error bars indicate 95% confidence interval determined by bootstrapping over the residuals.

successful males sire fit offspring of one or both sexes. This uncertainty hinges on whether or not sexual and natural selection act in the same direction, and arises from another central problem in evolutionary biology; what maintains genetic variation in fitness? In the context of sexual selection, there are two alternative perspectives. From one perspective, variation is maintained by a constant input of deleterious alleles through mutation, migration, or environmental change (which effectively changes adapted alleles into nonadapted ones). If mating success is biased against maladaptive alleles, whatever their origin, then sexual and natural selection will be congruent ("good genes" theory): males who are favored by sexual selection carry alleles also favored by natural selection and will therefore sire both sons and daughters of high fitness [1, 2, 10]. This hypothesis has support from a variety of theoretical models that have shown how sexual selection may enhance a species' overall fitness by increasing the rate of adaptation to novel environments [11, 12], the speed at which beneficial mutations are fixed and deleterious mutations are purged [13], thereby lessening the costs associated with sexual reproduction [14–16]. The alternate perspective is rooted on the long-standing [17] observation that that sexually selected traits come at a cost under natural selection, and the two processes are frequently in conflict. Under this scenario, maladaptive alleles are rare and make little contribution to the standing variation. Instead, much of the variation in fitness arises from sexual antagonism maintaining alternative alleles at intermediate frequency. Here, those alleles that make males successful are deleterious when expressed in daughters (e.g., [18–20]), so that sexual and natural selection are in opposition [3–5].

Both of these ideas are almost certainly true for some fraction of the genome [2, 21]. Therefore, the effects of sexual selection on fitness will ultimately depend on the nature of genetic variation present in a given population. For instance, a closed population with a long and consistent history of selection in a stable environment may be expected to be close to its adaptive peak and will have largely cleared most maladaptive alleles. Consequently, the primary contributor to genetic variation in fitness may then be those alleles maintained by various forms of balancing selection, including intralocus conflict. In such a population, we expect sexual and natural selection to be incongruent. However, many natural populations will not be so close to their adaptive peaks, either because of natural environmental fluctuations [22–25] or because of an influx of maladaptive alleles through migration [26]. In these populations the comparatively high frequency of maladaptive alleles

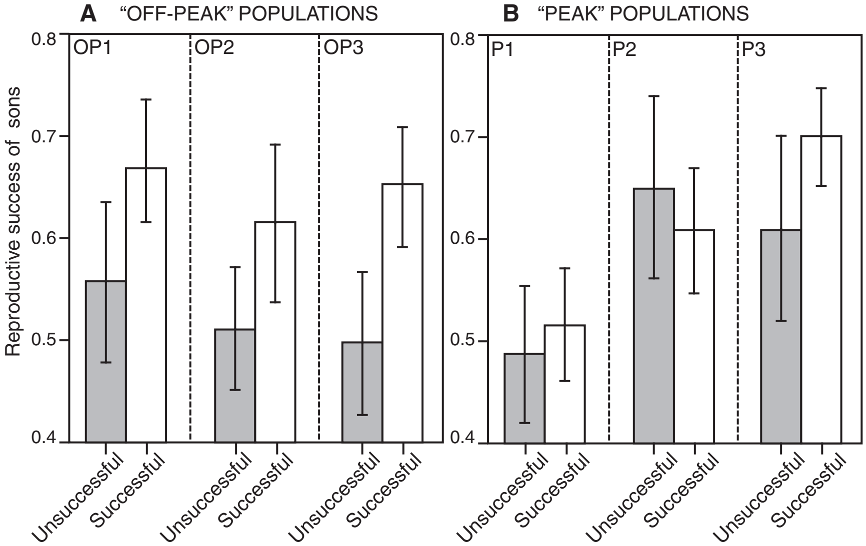

Figure 2. Effects of Sexual Selection and Evolutionary History on the Fitness of Male Offspring

Mean fitness of *D. melanogaster* sons sired by sexually "unsuccessful" and "successful" males in three replicate off-peak (A) and peak (B) populations, estimated from the statistical model. Error bars indicate 95% confidence interval determined by bootstrapping over the residuals.

will tend to make sexual selection concordant with natural selection through the "good genes" process.

Our study represents a formal test of the hypothesis that the effects of sexual selection on fitness depend on the type of variation in the population under study. Here, we mimicked populations with very different histories in an attempt to bracket the range of possibilities in nature, enabling us to assess the alternatives within a single experimental framework. Our results demonstrate that across this range, the indirect genetic effects of sexual selection are dramatically different. In our peak populations, where unconditionally deleterious alleles should have been whittled away by constant selection in a homogenous environment, we expected sexual antagonism to make a large contribution to standing variation. Consistent with this, successful males produced unfit daughters. In our off-peak populations, maladaptive alleles are making a larger contribution to the genetic variance. In these populations, successful males produced fit offspring of both sexes.

The observed difference in the effects of sexual selection is attributable to differences between populations in males rather than females. In the assays we used to classify males as sexually successful or unsuccessful, each focal male competed against a male from a common competitor stock for a female from another common competitor stock. Because "success" was measured in this common social environment, we can eliminate the possibility that the difference between treatments emerged because female preference changed. The question then arises what makes males successful in peak and off-peak populations that leads to differences in the effects of sexual selection? One possibility is that males in the two types of populations may differ in the traits they express (in means and/or variances), thus changing what is available to be sorted by sexual selection. A second possibility is that, in both population types, sexual selection favors a common trait, such as condition, but that condition has a different genetic make-up in the peak and off-peak populations. Male condition may be comprised of the combined effects of sexually antagonistic and sexually congruent alleles and the balance of these two differs between peak and off-peak populations.

One curious result was that in off-peak populations, successful males sired high-fitness sons, whereas in peak populations, successful males sired sons of average fitness. Why was there no correlation in fitness between males and their sons in peak populations? One intriguing possibility is based on intralocus conflict theory, which predicts that loci segregating for sexually antagonistic effects will be preferentially located on the X chromosome [27] (but see [28]). This prediction has received some support in lab-adapted populations of *D. melanogaster* [29, 30]. If substantial antagonistic variation is located on the X, successful males will transmit this chromosome to their daughters, depressing their fitness, but not to their sons. This predicted pattern is consistent with our data.

The observation that offspring sired by successful males developed more slowly than those sired by unsuccessful males was also unexpected. It may be better for males to take slightly longer to develop if slower development yields better-quality adults. There may be little selection against minor delays in development provided that eclosion occurs before some threshold time (i.e., when the egg-laying vials for the next generation are presented). Furthermore, development time is sexually dimorphic in *D. melanogaster* [31] and there has been some suggestion that there are male-specific fitness benefits associated with a slower maturation rates, possibly mediated by gonadal development [32]. This interpretation is supported in experimentally evolved populations where female-specific selection was removed and the resulting "masculinized" genomes produced phenotypes that were characterized by longer development times [33].

The results of our study may help to reconcile many of the apparent contradictions in the empirical literature and help answer the fundamentally important question of whether sexual selection is of net benefit to a species' evolution. Over the last 30 years there have been many studies that have examined whether sexual and natural selection act concordantly (see reviews in [1, 6–8]). The results have been mixed, but the reasons for this variation are unknown, because these studies vary in a large number of dimensions (e.g., study organism, experimental design, fitness metrics, selective history, etc.). If our hypothesis is correct, then much of this variation among studies may be accounted for by the amount and type of segregating variation in fitness. For example, the artificial introduction of new genetic variation with adverse effect(s) into a population, either by starting with an initially genetically variable population [34–36], backcrossing [37], mutation accumulation [38], or mutagenesis [39–41], may make the individuals off-peak with respect to their normal culture environment. Several of these aforementioned studies [34, 35, 37, 39, 40] have detected positive associations with sexual selection and fitness (or its major components) (but see [38] and [41] for exceptions). Likewise, the detection of a significant offspring viability benefit associated with mate choice observed by Partridge [42], but not detectable many years later in the same lab population of *D. melanogaster* [43], might be the unanticipated consequence of selection acting on genetic variation during the hundreds of generations that elapsed between these two studies. Additional scrutiny of the likely genetic diversity and composition of laboratory based studies that have shown no indirect benefits of nonrandom mating (e.g., [44, 45]) may be warranted.

In principle, an off-peak population can be created by placing a population in a new environment. For instance, Fricke and Arnqvist [36] compared the effects of sexual selection in experimental populations of seed beetles (initially created by mixing three populations of distinct geographic origin five generations prior to the start of the experimental evolution) that had been evolving either in their standard environment or on a novel host. Sexual selection accelerated adaptation in the novel environment but the effects of sexual selection were negative in the ancestral environment. However, not all studies examining populations in novel environments have found benefits to sexual selection [46–48]. There are several difficulties in interpreting these opposing results. First, many studies examine the combined effects of intra- and interlocus effects by measuring the productivity of male-female pairs, which is appropriate when assessing the net effect of sexual selection on population-level absolute fitness. The effects of the interlocus conflict (i.e., males and females directly harming one another) on a female's reproductive output can be large but are not relevant to the question of whether successful males sire fit offspring of one or both sexes. By directly assessing the fitness of a male's offspring, we have focused on the genetic benefits (or lack thereof) conferred by successful males. Specifically, we are asking whether successful males sire offspring of higher relative fitness than unsuccessful males, regardless of the total effect of sexual selection on population-level absolute fitness. Second, simply changing environments does not necessarily change variance in the intended manner. In the ancestral environment, deleterious alleles will be rare; some of these may be favored in the novel environment, but they will initially contribute little to the variance due to their rarity. Sexually antagonistic loci will still be highly polymorphic and may dominate the variance in fitness. A related third point is that most studies have examined the effects of sexual selection in either the ancestral environment or a novel environment. Without examining both together, it is impossible to determine whether the effects of sexual selection (in either sign or magnitude) differ between peak and off-peak populations. Finally, phenotypic expression of alleles may change in new environments (G × E) so that both sexually antagonistic and other types of variance will change in unpredictable ways. By directly manipulating the underlying variation rather than the test environment, our study avoids the unpredictable effects of G × E effects.

Our experiment was designed to span the range of possible states of natural populations to demonstrate the importance of evolutionary history in determining the effect of sexual selection on fitness. The results clearly show this to be the case. However, no lab study can tell us what is typical of natural populations. This brings us back to the crucial question of what maintains standing genetic variation in fitness in most natural populations. Although we have much theory, empirical work on the genetic architecture of fitness variation in the wild has only recently begun (e.g., [49–52]). Instead, our current understanding comes largely from laboratory studies; and our research indicates that population selection history should be taken into account when assessing the alignment of natural and sexual selection.

Supplemental Information

Supplemental Information includes Supplemental Results and Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.cub.2011.12.020.

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