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Misalignment of natural and sexual selection among divergently adapted *Drosophila melanogaster* populations

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The effect of sexual selection on nonsexual fitness is a major unanswered question in evolutionary biology that may have important implications for adaptation, diversification and the evolution of mate preferences. If reproductive success is condition dependent, the resulting sexual selection will tend to align with natural selection, promoting adaptation. One prediction under such a scenario is that adaptation to a novel environment should increase male mating success and hence sexual fitness. Environmentally induced plasticity in mate preferences could also contribute to an alignment of natural and sexual selection if the changes cause females to prefer locally adapted males as mates. We tested for both forms of alignment using a set of 10 independent populations of *Drosophila melanogaster* that were adapted to one of two environments. Competitive mating trials were performed between pairs of populations adapted to these two environments, with the trials designed to separate the effects of local adaptation on male mating success from plasticity of female mate preferences in response to these environments. Contrary to expectations under an alignment of natural and sexual selection, males did not have higher mating success when competing in the environment to which they were adapted. Furthermore, there was no evidence that females altered their mate choice based on their rearing environment, indicating the absence of any adaptive plasticity in mate preferences. Overall, despite previous evidence of reciprocal adaptation to these different environments, increased nonsexual fitness did not translate into higher mating success, indicating a lack of any alignment with natural selection of this component of male sexual fitness.

Natural selection can arise both from variation in nonsexual fitness (e.g. longevity, fecundity) and from variation in sexual fitness (i.e. differential success in mating and fertilization among reproductive individuals), with the latter process commonly known as sexual selection. In his original description of sexual selection, Darwin (1859) hypothesized that, because the most vigorous and best adapted males will tend to acquire the most mates, sexual selection may act to promote adaptation. More recently, theory suggests that the extent to which these two forms of selection align may also have major implications for population mean fitness (Lorch, Proulx, Rowe, & Day, 2003; Whitlock & Agrawal, 2009), niche diversification (van Doorn, Edelaar, & Weissing, 2009; Proulx, 1999, 2001, 2002) and the evolution of sex (Agrawal, 2001; Siller, 2001), among other things.

Building on Darwin's (1859) original idea, it has been suggested that sexual selection may align with selection arising from variation in nonsexual fitness (hereafter natural selection, for simplicity) because successful reproduction requires a substantial investment of time and effort, and includes direct and/or indirect competition with other members of the same sex (Andersson, 1994). Therefore, an individual's sexual fitness is likely to depend on their condition, as is expected for all major fitness components (Rowe & Houle, 1996; Whitlock & Agrawal, 2009). Individuals of high genetic quality (i.e. individuals well adapted to their environment) should acquire and use resources more efficiently to achieve a higher condition and should therefore have higher sexual fitness as well (Whitlock & Agrawal, 2009). As a consequence, condition-dependent sexual fitness should promote the transmission of locally adapted alleles.

Despite this expectation, data on the potential alignment of natural and sexual selection are mixed, with some studies finding evidence for alignment (Dolgin, Whitlock, & Agrawal, 2006; Hollis, Fierst, & Houle, 2009; Promislow, Smith, & Pearse, 1998; Radwan, 2004; Sharp & Agrawal, 2008), while others do not (Arbuthnott & Rundle, 2012; Correia, Yeaman, & Whitlock, 2010; Holland & Rice, 1999; Long, Pischedda, Stewart, & Rice, 2009; Martin & Hosken, 2004; Rundle, Chenoweth, & Blows, 2006). Sexual selection also generates the opportunity for sexual conflict arising from divergent reproductive interests of the sexes and can lead to the evolution of

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traits with sexually antagonistic fitness effects (Arnqvist & Rowe, 2005). The costs associated with such conflict may therefore reduce or even outweigh the benefits of mate choice and/or intrasexual competition in some systems (e.g. Long et al., 2009; Stewart, Hannes, Mirzatuny, & Rice, 2008; Stewart, Morrow, & Rice, 2005), potentially explaining some of the variation among studies (Rowe & Day, 2006; Whitlock & Agrawal, 2009).

Here we address the effects of adaptation on male mating success. While much attention has been given to studying adaptation to novel environments with respect to nonsexual fitness (e.g. Losos, Jackman, Larson, de Queiroz, & Rodriguez-Schettino, 1998; Sandoval, 1994; Schluter, 1993), its effects on male reproductive success are poorly understood. In many species, mating success is a major component of male sexual fitness that is likely to depend on the health or vigour of the males (i.e. is likely to be condition dependent). If sexual selection arising from variation in mating success tends to align with natural selection, one simple prediction is that individuals should have higher mating success in the environment to which they are adapted (i.e. in which they have higher nonsexual fitness; Dolgin et al., 2006). Surprisingly, there are few direct tests of this. Dolgin et al. (2006) and Correia et al. (2010) tested this prediction using independent sets of *Drosophila melanogaster* populations from two separate long-term selection experiments. In both cases, half of the populations were adapted to a cold temperature (18 °C or 16 °C, respectively) and the other half were adapted to a hot temperature (25 °C in both cases). Results were mixed, with increased mating success of males in the environment to which they were adapted in one set of populations (Dolgin et al., 2006) but not in the other set (Correia et al., 2010). The interpretation of these data were also complicated by the choice of environments (i.e. divergent temperatures) because, during mating trials, females must necessarily be exposed to the environment to which one of the two types of males are adapted. If female mate preferences are plastic with respect to these environments, increased mating success of males in their adapted environment could have arisen from divergent sexual selection generated by these different preferences rather than by the higher condition of locally adapted males, as recognized by Dolgin et al. (2006). More generally, plasticity of mate preferences may cause sexual selection to differ among environments, potentially altering its alignment with natural selection.

Female mate preferences can be affected by a diversity of factors, including age and reproductive experience (Bateman, Gilson, & Ferguson, 2001; Judge, 2010; Mautz & Sakaluk, 2008; Moore & Moore, 2001), season (Borg, Forsgren, & Amundsen, 2006; Milner, Detto, Jennions, & Backwell, 2010; Qvarnström, Pärt, & Sheldon, 2000), a female's condition (Cotton, Small, & Pomiankowski, 2006; Hunt, Brooks, & Jennions, 2005), predation risk (Csada & Neudorf, 1995; Hendrick & Dill, 1993) and learning (Amcoff, Lindqvist, & Kolm, 2013). While such plasticity has been observed under various conditions, its impacts on offspring fitness among environments have rarely been considered. This is surprising given the potential impact of plasticity on adaption to new environments and the alignment of natural and sexual selection (Price, 2006; Qvarnström, 2001). If female preferences are consistent across environments and target condition-dependent male displays, then the preferences themselves will be adaptive to females, causing them to mate with the best adapted males in any given environment. Under such a scenario, the preferred males may vary among environments due to changes in their underlying sexual displays as a consequence of their nonsexual fitness in a given environment. Alternatively, if female preferences change across environments, targeting different traits or different values of the same trait(s), then such plasticity will only be adaptive to females if it results in an increased preference for traits reflecting local adaptation in males. Importantly, such adaptive plasticity in mate preferences could contribute to the alignment of natural and sexual selection independently of condition-dependent male mating success (West-Eberhard, 2003). In addition, whether adaptive to females or not, males may evolve increased mating success during adaptation to a particular environment in response to the divergent sexual selection created by such plastic changes in female mate preferences, rather than because of their higher nonsexual fitness. Therefore, changes in male mating success and female preference in response to novel environments may have important implications for our understanding of the alignment of natural and sexual selection.

We evaluated the potential alignment of natural and sexual selection by examining male mating success across two novel environments in a way that allowed us to separate the effects of local adaptation of the males (i.e. their nonsexual fitness) and plasticity of female mate preferences in these environments. Our experiment took advantage of a long-term evolution experiment involving 10 replicate *D. melanogaster* populations, with five being adapted to the presence of salt in their food medium and the other five being adapted to the addition of the heavy metal cadmium. When assayed after 20 generations, these populations showed evidence of reciprocal adaptation such that nonsexual fitness was always higher for populations when tested in the environment in which they were evolved as compared to the other environment (Long, Rowe, & Agrawal, 2013). Using males from these different populations, we performed mating trials in a common garden experiment conducted separately within each environment. In this design, salt- and cadmium-adapted males competed for mates when both were raised in a salt environment and when both were raised in a cadmium environment, with females always being raised in a consistent (ancestral food) environment. If sexual selection arising from variation in male mating success aligns with natural selection, then males should have higher mating success when raised and tested in the environment to which they are adapted. In addition, to gain insight into plasticity of female mate preferences, we also used ancestral, nonadapted females in mate choice trials to estimate their preference for salt- versus cadmium-adapted males (each raised in their own environment) when these females were raised for a single generation in each of the two environments. If female mate choice is plastic, the outcome of these trials will vary based on the females' rearing environment, and if adaptive, females will more strongly prefer males raised in the same environment as them. Overall, we found no evidence for the alignment of natural and sexual selection, as neither male mating success nor female mate preference varied consistently based on the test environment. The lack of such alignment suggests that sexual selection, at least that arising from variation in mating success and the female preferences underlying this, will not necessarily enhance natural selection nor promote adaptation to new environments.

METHODS

Drosophila *Populations*

Our experiment used a set of replicate *D. melanogaster* populations from an evolution experiment began by A. Wang, C. C. Spencer, Y. Huang and A. F. Agrawal at the University of Toronto. For a detailed description of the history of these populations, see Long et al. (2013). These populations were established from a laboratory stock population, originally collected in 2005 in the Similkameen Valley, British Columbia, Canada (Yeaman, Chen, & Whitlock, 2010), that has been maintained at large population size on standard cornmeal/sugar/killed-yeast/agar medium. Following transfer to the University of Toronto, separate populations were exposed to