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Conflict between direct and indirect benefits of female choice in desert *Drosophila*

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Identifying the factors that contribute to the adaptive significance of mating preferences is one major goal of evolutionary research and is largely unresolved. Both direct and indirect benefits can contribute to mate choice evolution. Failure to consider the interaction between individual consequences of mate choice may obscure the opposing effects of individual costs and benefits. We investigate direct and indirect fitness effects of female choice in a desert fly (*Drosophila mojavensis*), a species where mating confers resistance to desiccation stress. Females prefer males that provide a direct benefit: greater resistance to desiccation stress. Mating preferences also appear to have indirect consequences: daughters of preferred males have lower reproductive success than daughters of unpreferred males, although additional experimentation will be needed to determine if the indirect consequences of female preferences actually arise from 'sexually antagonistic' variation. Nevertheless, the results are intriguing and are consistent with the hypothesis that an interaction between direct and indirect benefits maintains sexually antagonistic variation in these desert flies: increased desiccation resistance conferred by mating might offset the cost of producing low-fecundity daughters.

Keywords: sexual selection; sexual antagonism; female mate choice; direct benefits; indirect benefits

1. INTRODUCTION

Several models attempt to explain the adaptive significance of female preference and its consequences for the evolution of elaborate male secondary sexual characters (Kirkpatrick & Ryan 1991). Direct benefit models of sexual selection posit that females choose mates based on the quality of benefit to themselves (e.g. nuptial gifts, territory and parental care; Trivers 1972). In contrast, models of indirect benefits predict that preferred males confer greater genetic benefits to females' offspring through increased offspring survival (Fisher 1915) or increased mating success of sons (Fisher 1958).

Males and females maximize fitness through different sets of adaptations and may be subject to divergent selection pressures (Darwin 1874). Since most of the genome is shared between the sexes, genetic variants that benefit one sex can be costly to the other. Disruptive selection acting on the sexes can cause a negative correlation in fitness between males and females and potentially maintain 'sexually antagonistic' genetic variation for fitness within populations (Haldane 1962; Rice 1984). Sexually antagonistic variation has been documented in both laboratory and natural populations (Chippindale *et al.* 2001; Gibson *et al.* 2002; Fedorka & Mousseau 2004) and one study has indicated that female choice for the Fisherian benefits of good sons initiates the sexually antagonistic selection process (Fedorka & Mousseau 2004). Yet formal treatments suggest that the opposite pattern should emerge from Fisherian sexual selection; when opposing selection acts on the sexes, female choice will generally evolve to favour good daughters at the expense of sons (Seger & Trivers 1986; Albert & Otto 2005).

Much debate surrounds the importance of direct versus indirect benefits for the evolution of male traits (Janetos 1980; Partridge 1983; Rice 1988). Female choice for direct benefits does not preclude choice for indirect benefits. In the absence of direct benefits, female choice based on sexually antagonistic variation will evolve to favour males with good genes for daughters (Seger & Trivers 1986; Albert & Otto 2005). However, for females to prefer males with bad genes for daughters, males must directly increase the fitness of their mates to offset this indirect cost. Direct benefits of mating may permit the evolution of such preferences, particularly since direct benefits will tend to override any indirect fitness effects in offspring (Kirkpatrick & Barton 1997). We test this prediction in a desert fly, *Drosophila mojavensis*, in which mating increases female survival to desiccation stress—an important adaptation in an arid environment (Knowles *et al.* 2004, 2005).

2. MATERIAL AND METHODS

Drosophila mojavensis flies are from a single population (ABSF) described in Knowles & Markow (2001). All flies were reared on a banana–opuntia–agar medium and maintained at 28°C with a 12 h : 12 h light–dark cycle. Virgin adults were collected following eclosion and stored in sex-specific, wide-diameter yeasted culture vials. Only sexually mature flies were used (i.e. flies of 9 days of age), and matings were performed in the morning, the typical mating time in natural populations. One female was aspirated into a culture vial with a male and was observed for 30 min. Pairs that failed to mate within that time were discarded, which represented less than 10% of the pairs. Mated males and females were transferred to separate vials and retained for use in later parts of the experiment. All successfully copulating males began courting upon contact with the female. The 'no-choice' method has been used in mating experiments of other *Drosophila* species to control for male–male competition and does not interfere with physical and chemical interactions between the sexes used in mate choice involving other *Drosophila* species (Hedge & Krishna 1997; Koref-Santibanez 2001; Gowaty *et al.* 2002; Yenisetti & Hedge 2003), and it is appropriate for a preliminary examination of the roles of direct and indirect selection in influencing the evolution of female preferences in this species. Furthermore, it has been found for other insect taxa that the outcomes of tests are repeatable across females and are correlated with variation in long-term mating success, so the measure is not an idiosyncrasy of the method (Shackleton *et al.* 2005).

Males achieving copulation ($n=264$) were ranked by time until mating. Mating pairs from the upper and lower 30% of the ranks (females and their preferred and unpreferred males) were analysed for direct benefits ($n=157$). The remaining 40% were discarded. Indirect benefits were quantified for daughters for the upper and lower 15% of these males ($n=47$); due to small samples, the upper and lower 30% ranked males ($n=52$) were used to quantify indirect benefits via sons.

(a) *Measure of direct mating benefits*
Mated females were placed in a desiccation chamber maintained at approximately 0% humidity. This chamber was checked every 3 h and the survival times of females were recorded for a total of 123 h (the longest survival time of a mated female).

(b) *Measure of indirect mating benefits*
Each preferred and unpreferred male was then mated to a mature virgin female. The mated female was transferred to a fresh vial every day for 3 days (to avoid overcrowding of larvae) and the number of eggs laid counted. The total number of males that successfully produced eggs with their mates was $n=85$. The total number of emerged adult offspring in each vial was used to calculate the fecundity and offspring egg-to-adult viability for each female. Upon eclosion, offspring were collected and stored in sex-specific vials.

Virgin daughters ($n=949$) were each mated with a stock male and allowed to lay eggs for 3 days. The number of emerging adult offspring was used as a measure of the fecundity of each daughter. Virgin sons (three sons per vial; $n=150$ vials) competed against virgin yellow-bodied males ($y-$; six per vial) to mate with virgin yellow-bodied females ($y-$; six per vial). The proportion of emerging wild-type ($y+$) to yellow-bodied ($y-$) female offspring (y is X-linked) was used to measure the reproductive success of sons of a particular sire. While the design does not control for maternal family effects, such effects should be distributed randomly across preferred and unpreferred treatments, thereby not providing a systematic bias on the results.

(c) *Statistical analyses*
Female desiccation resistance was regressed against males' rank by female preference. Logistic regression, with rank as the categorical variable, was used to compare desiccation resistance to female choice. Considering female choice (time to mating) as an ordinal rather than a continuous variable is appropriate because it is non-normally distributed and because desiccation resistance was measured for mates of the upper and lower 30% of males. Nevertheless, linear regression of log-transformed data and rank correlation yield the same relationship between female choice and desiccation resistance. The fecundity of females, egg-to-adult viability and adult reproductive success of offspring was compared between preferred and unpreferred male sires using a *t*-test (two-tailed). We calculated the variance in the fecundity of daughters and the reproductive success of sons by scaling all values to 1 within each group in order to compare the variance in fitness traits for male and female offspring. Statistical analyses used JMP (v. 4.0, SAS Institute).

3. RESULTS AND DISCUSSION

To test whether female *D. mojavensis* choose mates for direct benefits, the degree of desiccation resistance conferred by mating with preferred and unpreferred males was compared (see §2). Females appear to choose mates for direct benefits. There was a significant positive correlation between female mating preference and resistance to desiccation stress (figure 1; logistic regression, $n=157$, $p=0.031$).

Offspring survival and reproductive success was measured to test for indirect benefits or costs of female choice (see §2). Sire type (preferred/unpreferred) did not affect female fecundity ($n=85$, $p=0.594$) or offspring egg-to-adult viability ($n=85$, $p=0.413$). However, offspring reproductive success differed between preferred and unpreferred males (figure 2). Daughters of preferred males have lower fecundity than daughters of unpreferred males (10% lower fecundity, $n=302$ daughters for the total offspring, $F_{1,300}=4.384$, $p=0.04$), whereas sons of preferred males have similar reproductive success to sons of unpreferred males ($n=150$ sons for the total offspring, $F_{1,148}=0.622$, $p=0.43$, and $n=52$). The variance in fecundity of daughters of preferred and unpreferred males is 0.017 and 0.019, respectively, significantly lower than the variance in reproductive success of
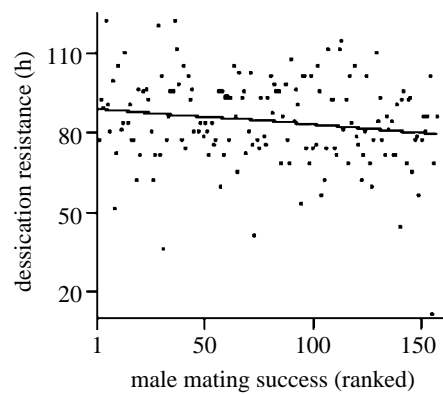

Figure 1. Preferred males confer greater direct mating benefits in terms of female desiccation resistance ($\chi^2=4.65$; $p=0.031$).
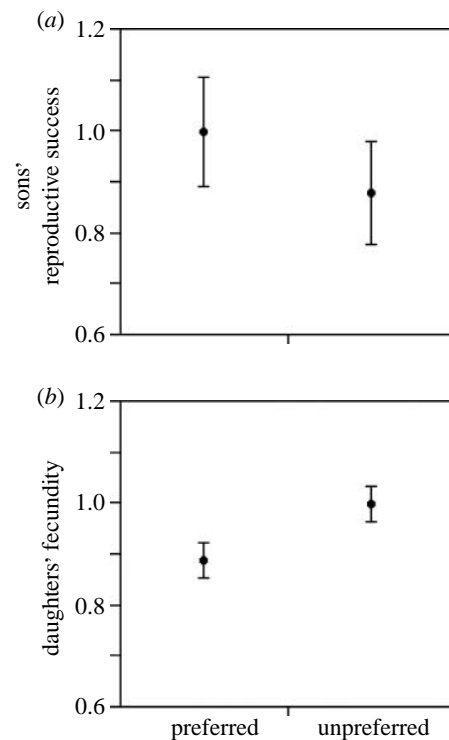

Figure 2. Daughters of preferred males have lower fecundity than daughters of unpreferred males ($p=0.04$), whereas sons of preferred and unpreferred males have similar reproductive success ($p=0.43$). Error bars represent the standard error.

sons (preferred = 0.248, unpreferred = 0.250). While we did not account for maternal family effects, such effects should be equally distributed across preferred and unpreferred males. While it is possible that females may differentially allocate resources to their offspring in response to male quality (Szentirmai *et al*. 2005; Velando *et al*. 2006), the fact that the female offspring of preferred males were significantly less fecund than those of unpreferred males suggests that this is not a likely confounding factor in our analysis.

The results suggest that female choice has direct consequences to female fitness as well as consequences to the fitness of her offspring—females mating with preferred males survive longer under conditions of desiccation stress, but have lower quality daughters. Furthermore, this loss is not recuperated through

benefit to their sons, as the sons of preferred males do not experience a higher reproductive success than those of unpreferred males. Since even small direct fitness consequences of mating are expected to overwhelm indirect consequences (Kirkpatrick & Barton 1997), the results imply that direct gains to females, rather than 'good genes' or 'sexy son' benefits, primarily influence the evolution of choosiness in this species.

(a) *Is genetic variation sexually antagonistic?*

The reproductive success of fathers relative to daughters—i.e. successful fathers have unsuccessful daughters—is indicative of sexually antagonistic genetic variation. This suggests that an interaction between direct and indirect benefits may maintain sexually antagonistic fitness variation in these desert flies. By favouring males that increase their mates' resistance to desiccation stress, female choice counteracts selection against genes that are harmful to females. Female choice can therefore give rise to sexually antagonistic selection, a process that maintains genetic variation under a wide range of conditions (Kidwell *et al.* 1977; Rice 1984).

If genetic variation is sexually antagonistic, why is the reproductive success of sons unrelated to that of their fathers? If sexually antagonistic variation is X-linked (as it appears to be in *Drosophila melanogaster*; Gibson *et al.* 2002), sons will not express 'good male' phenotypes because each inherits a maternal X chromosome. Another possibility is that the genetic variation underlying offspring reproductive success may have a larger impact on females than on males (as often occurs with quantitative traits in *Drosophila*; Mackay 2004). Such sex-by-genotype interactions give rise to a detection bias in favour of daughters. Although the sample size for the reproductive success of sons is small, the variance in this trait was significantly larger than that of female offspring fecundity, suggesting that this result is not indicative of small sample size alone. Future work with this species can disentangle these interesting possibilities by conducting additional offspring fitness assays and by examining whether there is any fitness heritability between maternal grandfathers and grandsons.

These results demonstrate that interactions between direct and indirect selection on female choice may be complex and that additional experimentation is needed to identify how sexual selection might be operating in these flies. For example, it will be interesting to determine if the lack of significant differences between the fitness of sons from preferred and unpreferred males is an artefact of sample size and to test whether an effect of male fitness will become evident with additional study. Furthermore, future study should control for maternal family effects, which this preliminary study did not do. Nevertheless, the results suggest that understanding the dynamics of sexual selection will require analysis of selection operating across generations and between the sexes. Moreover, these results raise the intriguing possibility that genetic variation in traits under strong sexual selection (e.g. 'the paradox of the lek' (Borgia 1979)) may be due to indirect consequences of mating.

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