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# Female mate preferences in *Drosophila simulans*: evolution and costs

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## Abstract

Female mate preference is central to sexual selection, and all indirect benefit models require that there is genetic variation in female preference. This has rarely been tested however, with relatively few studies documenting heritable variation in female preference and even fewer that have directly selected on mate preference to unequivocally show that it can evolve. Additionally, costs of mate preference are poorly understood even though these have implications for preference evolution. We selected on female preference for *ebony*-males in replicate *Drosophila simulans* lines, and generated a rapid evolutionary response in both replicates, with the proportion of females mating with *ebony*-males increasing from approximately 5% to 30% after five generations of selection. This increase was independent of changes in *ebony*-males as only females were included in our selection regime. We could detect no cost to mate preference itself other than that associated with the fitness consequences of mating with *ebony* males.

## Introduction

Sexual selection was proposed by Darwin (1871) to explain the evolution of characters that appeared to be detrimental to survival. Darwin also identified the main mechanisms of sexual selection, female choice and male–male competition. While much of the theory of sexual selection was accepted soon after its publication, female preference was controversial (O'Donald, 1980; Maynard Smith, 2000). A few years after Darwin's (1871) publication for example, Dewar & Finn (1909) suggested that it was 'absurd to credit birds with aesthetic tastes equal, if not superior, to those of the most refined and civilized of human beings'. In spite of this hostility and a long time-lag, female preference for certain male phenotypes has now been documented in many taxa (e.g. Ryan, 1983; Moore & Moore, 1988; Wilkinson & Reillo, 1994; reviewed in Andersson, 1994; Moore & Moore, 2006) and the potential importance of female preference has been verified in a range of sexual selection models (e.g. Lande, 1981; Kirkpatrick, 1982; Iwasa *et al.*, 1991; Pomiankowski *et al.*, 1991; reviewed in Mead & Arnold, 2004; Kokko *et al.*, 2006). Many of these models focus on indirect benefits of female choice, and the genetic correlation between female preference and the male traits targeted by preference is central to these indirect-benefit models. The basic logic is that if some females prefer males with extreme traits, then this nonrandom mating will generate a genetic correlation between trait and preference if there is a heritable component to the male sexual ornament and female mate preference (Fisher, 1930). The strength of this genetic correlation can profoundly influence evolutionary trajectories. For example with strong covariance, runaway can ensue as preference and ornament evolve exponentially in a burst of rapid evolution that ends when natural selection against the male trait becomes sufficiently strong or genetic variation is exhausted (Lande, 1981). Over a wide range of conditions, the genetic correlation approximates to $\beta = aG_PG_T$, where $\beta$ is the genetic covariance at equilibrium, $G_P$ is the genetic variance in preference, $G_T$ is the genetic variance in the male attractiveness and $a$ is the effectiveness of the male sexual signal and female preference at generating nonrandom mating (Bakker & Pomiankowski, 1995). Obviously, genetic variation in female preference is needed for the genetic correlation to build up, and then, even if there is no direct selection on female preference, preference can evolve via its

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association with male sexual traits, with increased preference selecting for further trait exaggeration and so on (Fisher, 1930; Lande, 1981). However, in spite of the central role female preference plays in sexual selection (Heisler, 1984a; Bakker & Pomiankowski, 1995; Chenoweth & Blows, 2006), and in the importance of genetic variation for preference, preference is still relatively poorly studied. This has prompted repeated calls for more investigations of the genetic variation in female preference (e.g. Heisler, 1984a; Bakker & Pomiankowski, 1995; Wagner, 1998; Bakker, 1999; Mead & Arnold, 2004), as a general lack of variation in preference would require a serious revision of our current understanding of sexual selection (Bakker & Pomiankowski, 1995; Mead & Arnold, 2004).

Direct selection on female preference, either via fecundity or longevity costs, has also been shown to be important in models of sexual selection (Mead & Arnold, 2004), particularly because indirect effects, such as those generated by the correlation between preference and trait, are likely to be small relative to direct effects (Kirkpatrick & Barton, 1997). Furthermore, Lande's (1981) model of runaway assumed no direct selection on female preference, and when direct selection on preferences was initially incorporated into genetic models of sexual selection, single point equilibria frequently resulted, and runaway was therefore considered unlikely (e.g. Iwasa *et al.*, 1991; Pomiankowski *et al.*, 1991). However, more recent investigations suggest that these equilibrium points may be unstable and even with direct selection on female preference, runaway can still occur (e.g. Hall *et al.*, 2000; reviewed in Mead & Arnold, 2004). It has also been suggested that costs of preference are likely to be ubiquitous through pleiotropic effects of preference genes or search costs associated with preference for certain males (Kirkpatrick & Ryan, 1991; Ryan, 1997; Hall *et al.*, 2000), and costs of preference have been documented (e.g. Englehard *et al.*, 1989). Nonetheless, although there are many investigations of costs of mating (e.g. Martin & Hosken, 2004), there is little empirical data on preference costs or direct selection on preference, prompting calls for more effort in estimating them (Wagner, 1998; Hall *et al.*, 2000; Mead & Arnold, 2004). Unfortunately, it is difficult to assess costs of preference beyond those associated with mating with particular males (Maklakov & Arnqvist, 2009), but in spite of this, investigations of potential preference costs are sorely needed (Heisler *et al.*, 1987; Maklakov & Arnqvist, 2009).

One way to unequivocally document genetic variation in female preference is to select on it (Bakker & Pomiankowski, 1995), and this is the approach we use here with *Drosophila simulans*. We have previously investigated the genetics of sexual selection in this species, primarily from a male perspective, to show that male attractiveness is heritable (Taylor *et al.*, 2007) and positively associated with sperm competitiveness (Hosken *et al.*, 2008). Additionally, there does not appear to be any direct selection on female preference because female fecundity is not directly influenced by their choice of mate (Taylor *et al.*, 2008a,b, 2010). However, this inference was based on counts of offspring produced rather than eggs laid, and as such, may partially confound offspring fitness with female fitness (Wolf & Wade, 2001). Here, we first used iso-female lines to test for genetic variation in one measure of female mate preference. We then used artificial selection and experimental evolution to further investigate female preference and potential costs of preference. Although we find that there is variation in preference across isolines and that female preference evolves rapidly when subjected to selection, we could find no costs to preference beyond those associated with the quality of females' mates.

## Methods

### Fly stocks

The base-line wild-type populations of *D. simulans* used here were derived from twenty iso-female lines supplied by the Centre for Environmental Stress and Adaptation Research, La Trobe University, Australia. These were collected from the wild in 2004. They had been maintained in large population cages (ca. 800–1000 flies/cage) with overlapping generations for 4 years prior to the start of this investigation and have been found to harbour considerable genetic and phenotypic variation (e.g. Taylor *et al.*, 2007, 2008a; Wright *et al.*, 2008). The *ebony* stock population was established using a strain obtained from the Tucson stock centre and was maintained as above for over 50 generations. *Ebony* is a phenotypic body-colour mutant with reduced fitness. *Ebony* flies are partially blind, often have courtship defects (including licking females less and altered courtship song), and males are frequently more aggressive (Søndergaard, 1985). All flies were reared on 'Drosophila quick mix medium' (supplied by Blades Biological, Edenbridge, Kent, UK) at 25 °C and a 12 : 12 h light:dark cycle. Subsequent housing conditions followed this regime unless stated otherwise. Flies to be used in preference selection lines (and subsequent preference cost assays) were initially collected as virgins from stock population laying vials (*ebony* and wild type: housed separately). Briefly, laying pots were left in the population cages overnight and then removed and housed under standard conditions (25 °C: 12 : 12 light). Virgin flies emerging from the laying pots were separated and housed by sex (< 10 flies per vial) with an excess of the culture medium for 3 days before initial pairings to start the selection lines.

### Isolines

We used six of our original isolines and collected 60 virgin males and females from each. Again we collected

emerging virgin adults and housed them by sex (within isoline) at densities of no more than 10 flies per vial, with an excess of the culture medium for 3 days prior to experimental pairings. When flies were 3 days old, females from each line were paired with males (i.e. one female was placed with one male) from each line in a fully factorial and balanced design. We measured the time it took for a female to copulate with a male (copulation latency) as our indicator of preference (time from introduction of male to mating – this correlates with time from first courtship to mating but is easier to measure: Taylor *et al.*, 2008a). This is one standard measure of female preference in *Drosophila* (e.g. Speith, 1974; Ritchie *et al.*, 1999; Acebes *et al.*, 2003) and is consistent with preference definitions as it reflects the tendency for females to mate with certain males (Heisler *et al.*, 1987; Jennions & Petri, 1997). Additionally, male *Drosophila* cannot force copulation in nonteneral females (Eberhard, 2002) but use a range of courtship behaviours (e.g. Pitnick, 1991; Droney, 1996; Ritchie *et al.*, 1999; Acebes *et al.*, 2003) that a female interrupts with her own acceptance or rejection signals (Speith, 1974). As such, hardened females primarily determine whether or not copulations occur in *Drosophila* (Markow, 1996). Because females determine when copulation occurs, we reasoned that females should copulate faster with more attractive, preferred males. Additionally, measuring preference this way excludes any potential for male–male competition to interfere with female choice. Mating latency (log transformed) was then analysed using univariate GLM with female and male isolines as random factors. We also note that although it is possible to calculate heritabilities from isolines, this should ideally be done within five generations of line establishment (Hoffmann & Parsons, 1988). Because our lines had been in captivity for much longer than this, we did not calculate preference heritability using these data. Nonetheless, differences across isolines would indicate genetic variation in female preference (Hoffmann & Parsons, 1988).

### Selection lines

Here, we selected on *ebony* female preference for *ebony* males in two independent populations (lines) and maintained a single control line at the same average population size as the selection lines. In the selection lines, only *ebony* females that mated with *ebony* males were used to found each subsequent generation, whereas in the control line, females were chosen at random and therefore probably predominantly included females with preference for wild-type males (ca. 95% of stock *ebony* females mated with wild-type males when given a choice). Although this is a highly artificial system, it does demonstrate how preference could evolve and also allows us to investigate potential costs of preference.

On the day of mating, virgin males (collected as virgins from the stock populations each generation of testing) were transferred into the mating vials without any anaesthesia (de Crespigny & Wedell, 2008). We measured female preference by exposing females (100 per line) to pairs of males (one wild-type, one *ebony*) for a maximum of 3 h and scored which male a female mated with. Female preference measured this way is consistent with preference definitions: preference reflects the propensity for females to mate with certain males (Heisler *et al.*, 1987; Jennions & Petri, 1997; and see *Isoline* section above). While this allows for male–male competition, which can potentially confound female mate choice, our selection regime allows us to take this into account. Every generation tester males were derived from our two stock populations (*ebony* and wild-type), and hence there was no opportunity for adaptation to occur in the males (in response to female preference). This also means that if our measure of mate preference was solely because of male–male interactions, or males more generally (i.e. there was no female genetic variation in our measure of preference), then there would be no change in female preference over time. The fact that there was a response indicates that our measure of preference is capturing some component of females' mate preference.

Soon after copulation was complete, males were removed from the vial and in the selection lines, females that mated with *ebony* males were allowed to oviposit for 24 h. Subsequent generations of females in the selection lines were derived from the offspring obtained from these matings and were tested in the same way each successive generation. Females providing offspring for the control line were chosen at random, but the census size of control dams was deliberately kept at the mean selection line number (see Fig. 3).

After five generations of selection, realized heritabilities were calculated using Falconer's (1981) method for threshold traits. With this method, the two phenotypes, mating with *ebony*/not-mating with *ebony*, are assumed to be because of an underlying, continuous trait referred to as liability. Liability is normally distributed and is measured in standard deviation units. Individuals above a certain threshold show a certain phenotype, whereas those below it show another (mating with *ebony*/not-mating with *ebony*) (Falconer, 1981). Because liability is continuous, it is amenable to standard quantitative genetic analyses and trait heritability is then calculated from the cumulative response to selection (e.g. Radwan, 2003). This is the recommended method for calculating preference in binary choice trials such as we use here (Bakker, 1999).

After selecting on preference, documenting a response and estimating its heritability, we randomly (with respect to preference) selected 100 virgin (*ebony*) females from each selection line and housed them with 100 virgin *ebony* and 100 virgin wild-type males in population cages (one for each line). Excess food was provided, and free mate choice and overlapping generations were allowed.

This relaxed the strong directional selection on preference we had previously imposed. After two generations of relaxed selection, *ebony* female preference for *ebony* males was again assessed. This allowed us to estimate the decay of preference and hence preference costs in the absence of direct selection favouring female preference for *ebony*. However, because *ebony* flies have lower general fitness than wild-type flies, we needed to estimate the direct fitness costs of mating with *ebony* males to assess any potential costs associated with the preference itself. To do this, crosses between *ebony* females and *ebony* and wild-type males were conducted. The relative fitness of *ebony* flies was calculated using the number of offspring to emerge within 7 days after first eclosions from vials in which singly mated females had laid for 24 h. This relative fitness measure was then used to predict a rate of preference decay when selection was relaxed. This is easily carried out from generation 1–2 as only *ebony* and wild-type flies are present at generation 1, but in subsequent generations, calculations become complicated by the presence of various heterozygotes and backcrosses. Hence, we only compared preference decay at generation 2. We found that *ebony* × *ebony* crosses had a relative fitness of 0.51 and conservatively assuming the fitness of heterozygotes (*ebony*/wild-type crosses) to be the same as the wild-type females (see Dobzhansky, 1947; Moree & King, 1961), the relative fitness of *ebony* preferring females from generation 1–2 of relaxation was 0.58 (this includes heterozygous females that preferred *ebony* males and *ebony* homozygous females that preferred *ebony* males). In the absence of any additional costs, the decay in female preference for *ebony* once we relaxed selection would be purely because of this fitness deficit of the *ebony*-preferring females (Table 1). Note we ignore all potential indirect effects as they will be small relative to direct effects (Kirkpatrick & Barton, 1997). We note that this aspect of the study is not particularly strong. For example, by estimating cost over only two generation, we could confound costs with epistasis for preference (relaxing selection could lead to recombinational breakdown of more favoured complexes of preference genes and hence rapid decay might not indicate costs *per se*: but see Results), and just because we saw a rapid response to selection we may not see a rapid decay. Nevertheless, we include this component here as an example of how such costs could, *in principle*, be assayed.

**Table 1** Expected decay of *ebony* preference in the experimental populations based on an estimated relative fitness of 0.51 for *ebony* preferring females from generation 0 to 1 and of 0.58 from 1 to 2.

| Generation | 0 | 1 | 2 |
|---|---|---|---|
| Rep. 1 | 32.63 | 16.64 | 9.65 |
| Rep. 2 | 28.88 | 14.73 | 8.54 |

## Results

### Isolines

Analysis of the female preference (latency to mate) across the isolines revealed significant differences across female ($F_{5,324} = 12.26$; $P < 0.001$) (Fig. 1) and male genotypes ($F_{5,324} = 3.98$; $P = 0.002$). The interaction between male and female identity was also significant ($F_{25,324} = 2.93$; $P < 0.001$) (Fig. 2). This indicates that there is genetic variation in this measure of female preference in our population (Fig. 1) that was not simply because of differences in female receptivity, because there were also male identity effects. Additionally, the interaction indicates female responses depended on male identity, and not all female genotypes agreed on the attractiveness of each male genotype.

### Selection lines

There was a steady increase in the number of females preferring *ebony*-males as mates. In the base population only about 5% of females mated with *ebony*, and this proportion remained more or less constant in our control line (Fig. 3). In the selection lines however, there was an increase over time to about 31% of females choosing *ebony* by generation 5. The realized heritability of preference averaged across replicates was $h^2 = 0.26 \pm 0.11$ (0.24 and 0.28 in each line).

Based on the relative fitness of the *ebony*–*ebony* cross, 9.7% of females in line 1 were predicted to prefer *ebony* 2

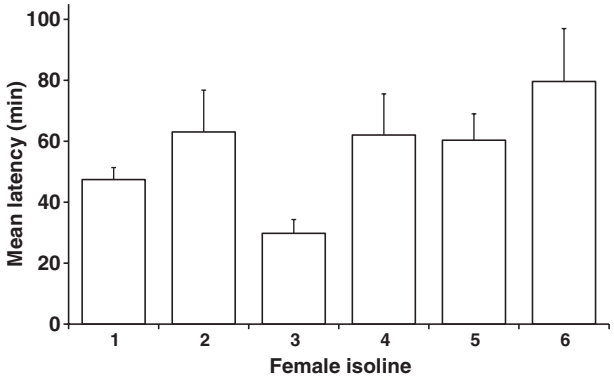


**Fig. 1** Mean (±SE) female preference for six *Drosophila simulans* isofemale lines (wild-type). Preference was measured here as mating latency (means for 60 females per line). Shown here are the untransformed data. Significant differences between lines (*post hoc* tests of log-transformed latency – Fisher's PLSD: 3 < 1–6; 1 < 6; 5 < 6; 2 < 6. Tukey–Kramer: all significantly differ) indicated there is genetic variation for this measure of preference, and note that there were also significant effects of male genetic background and an interaction between female and male genetic background (see Fig. 2).

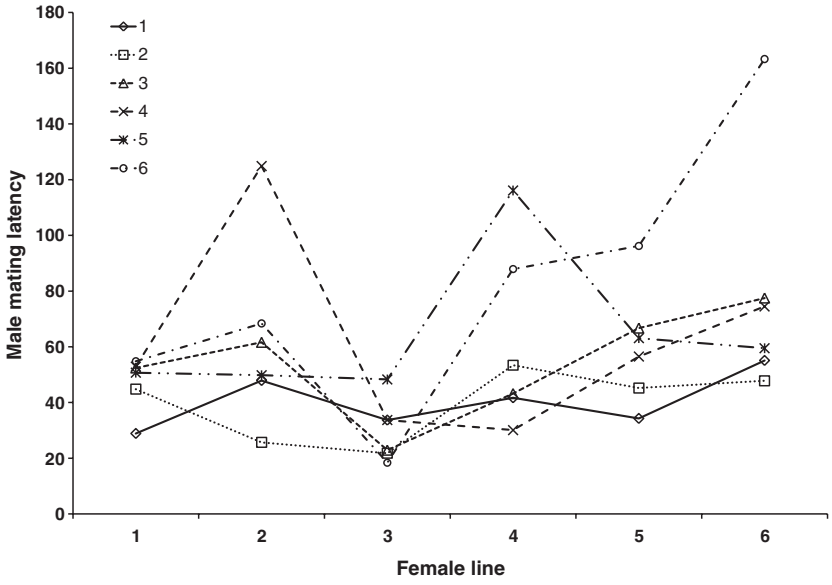


**Fig. 2** The interaction between male and female genotype influencing female preference assessed using wild-type isofemale lines. Preference was measured here as mating latency. On the *x*-axis are the same six isolines shown in Fig. 1, with specific responses to each male genotype (the points connected by a line: i.e. all diamonds represent males from isoline 1, open squares males from isoline 2, and so on. See Figure inset). This interaction between male and female genotypes was statistically significant.

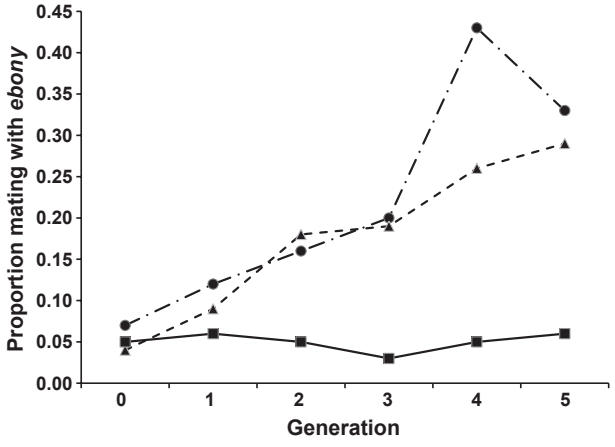


**Fig. 3** Changes in the proportion of females preferring to mate with *ebony*-males over five generations of selection. Dashed lines (joining triangles and circular symbols) are the two upward selection replicates, whereas the solid line (connecting the solid squares) is the unselected control. Only females were included in the selection regime (all males came from populations cages every generation) and the control line was maintained at the same census size as the average of the selection lines.

generations after relaxation of selection, whereas for line 2 the corresponding prediction was 8.5%. The observed values were 15% and 12%, respectively. Although the observed values were slightly higher than predicted (i.e. decay was slower than predicted), contingency tests indicated differences were not statistically significant (both $\chi^2 < 1.15$; both $P > 0.28$).

## Discussion

Our main finding was that selecting on female preference for *ebony* males generated a steady increase in the proportion of females mating with these males, and our estimate of preference heritability was moderate. We also found that isolines differed in another measure of female preference, the speed at which females mated with a male (latency to mate), which also indicates there is genetic variation in female preference. However, we found no evidence for preference costs over and above the cost of mating with *ebony* males. We discuss each finding and their main consequences in turn.

Female preference can be measured in a number of ways, but it is generally agreed that preference reflects a female's inclination to mate with certain males (Heisler *et al.*, 1987; Jennions & Petri, 1997). In accordance with this, we assessed female preference in two ways and found genetic variation for both measures, including unequivocal evidence that preference can evolve. Genetic variation for female preference has previously been documented in a small number of taxa (e.g. O'Donald & Majerus, 1985; Moore, 1989; Ritchie, 1992; reviewed in Bakker, 1999), including *Drosophila* (e.g. Heisler, 1984b; Scott, 1994; McGuigan *et al.*, 2008). Previous estimates of preference heritability are generally lower than 60% (Bakker, 1999), which is what we find here assuming preference is polygenic, which it seems to be (based on the responses seen). Most models of sexual selection also assume preference is polygenic and consistent with this, there is evidence in *Drosophila* that multiple chromosomal regions contribute to complex behaviours like mating, attractiveness and mate preference (Kawanishi & Watanabe, 1981; Heisler, 1984b; Mackay *et al.*, 2005;

Gleason *et al.*, 2009). It is worth noting that preference was also significantly heritable if we assumed it was determined at a single locus (data not shown).

Genetic variation in preference is essential for models of indirect mate-choice benefits, and the current study provides evidence for genetic variation in female preference in *D. simulans*. We have previously found no evidence of good genes or direct benefits/costs to mate choice in our wild-type population (Taylor *et al.*, 2008a,b, 2010) but have documented genetic variation in male attractiveness (Taylor *et al.*, 2007; Hosken *et al.*, 2008), which indicates that Fisherian benefits are probably the only benefit available to females via their choice of mate in our population. Direct testing of this requires that we identify the precise male characters on which females make their choices. This is something we are currently undertaking, with cuticular hydrocarbons and song likely to be important (e.g. Speith, 1974; Blows & Allan, 1998; Ritchie *et al.*, 1999). However, when there is genetic variation in male attractiveness and female preference (which we find), nonrandom mating (which we also find), and the strength of other selection acting on each trait is relatively weak, it is difficult to see how Fisherian effects can be avoided (Shuster & Wade, 2003; and see Lande, 1981). We nevertheless emphasize that what we document in our study population need not be indicative of natural populations of *D. simulans*, nor does the genetic variation we document in preference indicate preference polymorphism exists in nature (i.e. we are not claiming what we see in the laboratory is necessarily equivalent to the wild). This remains to be investigated. We also note once more that the isoline results indicate genetic variation in female preference (the significant female identity effect), but this was not simply because of receptivity differences between isolines as there were male identity effects and an interaction between female and male genotypes. Thus, female preference depended on male identity, but not all female genotypes agreed on the relative attractiveness of male genotypes. This is precisely what is required to build up a genetic correlation between male attractiveness and female preference.

Genetic variation in female preference has rarely been documented (Bakker, 1999; Mead & Arnold, 2004) and estimates of preference costs are even rarer (Heisler *et al.*, 1987; Maklakov & Arnqvist, 2009). Costs of preference can come in many forms, but of particular interest are direct costs to females because of differences in their mating preference (Heisler *et al.*, 1987; Maklakov & Arnqvist, 2009). We tried to estimate this latter cost by measuring how quickly preference for *ebony* males was lost from our selection lines once the absolute advantage of *ebony* preference was removed. We found no indication that preference decayed at a rate faster than that predicted based on the relatively lower fitness of females mating with *ebony* males. If anything the declines were slower than predicted (although not significantly so). Thus, although *ebony* preference declined once selection was relaxed, the rate of decline did not indicate that *ebony* preference itself was particularly costly under our experimental set-up. There were potential indirect costs here too as *ebony* sons were not as attractive as wild-type sons in the relaxed-conditions population cages. However, indirect effects ought to have much weaker effects than direct effects (Kirkpatrick & Barton, 1997), so it is perhaps no surprise that we detected nothing that could be interpreted as an indirect cost of *ebony* preference. Similarly, in our population cages, direct costs of being choosy may be minimal as flies are at relatively high density and females are surrounded by males, potentially minimizing all preferences costs. Consequently, the fact that we did not find costs of preference above those because of being *ebony* is perhaps not surprising, and our statistical power was not great. Additionally, as we noted earlier (Methods), this component of the study was not particularly strong for a number of other reasons (e.g. two generations may not be enough to detect decay). Hence, there may be costs to having different mate preferences that we could not detect. However, our failure to detect major costs of preference is at least consistent with previous laboratory studies of this population that did not employ the *ebony* mutant (Taylor *et al.*, 2008a,b, 2010) and supports our supposition that indirect benefits, even small ones, could maintain choice in this system.

In summary, we found unequivocal evidence for genetic variation in female preference but could not detect costs associated with preference. We now need to identify the precise traits influencing male attractiveness in our population, but currently, Fisherian benefits seem adequate to maintain choice in this system.

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