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Genotype-by-environment interactions for female preference

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Abstract

Sexual selection is responsible for many of the most spectacular displays in nature, and female preference for certain males is central to much of this. However, female preference is relatively poorly understood, particularly the relative importance of a female's genes, the environment and their interaction on her preference. We investigated preference in a no-choice design using *Drosophila melanogaster* iso-female lines and find that there are genotype-by-environment interactions for female preference. Whereas the choosiness of some female genotypes differed little across environments, that of others differed greatly, so that the choosiness rank of females in one environment did not necessarily predict their rank in another. Furthermore, the genetic variance underlying preference also varied across environments. These findings have important consequences for the evolution of female preference and the male sexual traits preference targets.

Introduction

Female mate preference is central to the operation of sexual selection and is responsible for the evolution of some of the most spectacular morphology and behaviour in nature (Darwin, 1871; Arnold, 1983; Kirkpatrick, 1987; Andersson, 1994). Female preference was a controversial aspect of Darwin's sexual selection thesis (Cronin, 1991), but has now been documented in many taxa (Andersson, 1994; Jennions & Petrie, 1997). It is defined as the properties that influence a female's propensity to mate with certain males, and preference at least partly determines a female's choice of mate (Heisler *et al.*, 1987; Kirkpatrick, 1987; Jennions & Petrie, 1997). Preference can be further subdivided into choosiness, the time taken to examine each mate and preference functions, the order in which males are ranked (Jennions & Petrie, 1997). These two determinants of preference are important because they can be measured empirically (Jennions & Petrie, 1997), and this is frequently carried out using a no-choice design to eliminate the potential confounds of male–male competition (e.g. Houde & Torio, 1992; Gowaty *et al.*, 2002; Jones & Quinnell, 2002; Shackleton *et al.*, 2005; Tregenza *et al.*, 2006). Nevertheless, in spite of the importance of female mate preference for sexual selection, there have been relatively few investigations of genetic variation in preference (e.g. Moore, 1989; Sharma *et al.*, 2010; reviewed in Bakker & Pomiankowski, 1995; Jennions & Petrie, 1997; Mead & Arnold, 2004), even though this is an obvious prerequisite for mate preference to evolve (Arnold, 1983; Bakker & Pomiankowski, 1995; Mead & Arnold, 2004). Additionally, there have been few investigations of the environmental sensitivity of female preference, or more importantly, if this varies with female genotype to generate genotype-by-environment interactions (GEIs) for preference (Ingleby *et al.*, 2010).

GEIs generally are likely to be ubiquitous, and for male sexual traits are well documented in a few key systems (Bussière *et al.*, 2008). While GEIs provide one solution to the lek paradox (Tomkins *et al.*, 2004; Hunt *et al.*, 2004; Radwan, 2008; Bussière *et al.*, 2008), the existence of these interactions has many other implications. This is especially true for sexual selection because most formal modelling of this process assumes environmental constancy, either implicitly or explicitly (Greenfield & Rodriguez, 2004). This assumption ensures that signals are reliable, but with the addition of even small GEIs, predicted positive associations between sexual-trait size and male quality can be reversed (Higginson & Reader, 2009). In spite of this, however, temporal or spatial

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correlation between environments, or a small probability of signal reliability may be enough to maintain female preference for specific male characters. Things may be more complicated if both male trait and female preference are subject to GEIs (Ingleby *et al.*, 2010), if only because genetic correlations between male trait and female preference are central to all models of sexual selection that assume indirect benefits of choice (Heisler, 1994), and GEIs can potentially break or weaken this covariance.

We investigated potential genotype–environment interactions for female preference in *Drosophila melanogaster* using a genotype-by-environment design where females from nine iso-females lines were reared either under normal temperatures or cold exposure. When females were sexually mature, we measured their preference for males from six unrelated isolines. As noted earlier, preference is broadly accepted to reflect a female's propensity to mate with certain males (Kirkpatrick, 1987; Jennions & Petrie, 1997; Kirkpatrick *et al.*, 2006). Additionally, because male *Drosophila* cannot force copulations (Eberhard, 2002), females should mate faster with more attractive, preferred males (Speith, 1974; Kyriacou & Hall, 1986; Ritchie *et al.*, 1999; Acebes *et al.*, 2003; Taylor *et al.*, 2007; Hosken *et al.*, 2008; Sharma *et al.*, 2010 – for further discussion see Materials and methods and Taylor *et al.*, 2009). We therefore assessed female preference in two ways: as a female's willingness to accept a mating (mate acceptance) and, if a mating occurred, how quickly females copulated with a male (latency to mating). These measures capture the two critical aspects of female preference discussed above: latency reflects choosiness (defined as the time females take examining males before mating: Jennions & Petrie, 1997), and because female genotypes are exposed to the same multiple male genotypes, acceptance is a measure of the preference functions (the order in which males are ranked by females: Jennions & Petrie, 1997) as well as reflecting choosiness. Additionally, by adopting the standard no-choice design (e.g. Shackleton *et al.*, 2005), we remove potential confounds of male–male competition, and it should be noted that identical outcomes have been recorded in choice or no-choice assessments of female preference in *Drosophila* (e.g. Avent *et al.*, 2008; Taylor *et al.*, 2008).

Materials and methods

Drosophila melanogaster lines

Drosophila melanogaster used in this study were collected from North Carolina (by Trudie Mackay in 2004 and donated to us by Frank Jiggins in 2007). Lines have been maintained by full-sib (brother-sister) matings for more than 20 generations and as such are theoretically predicted to be homogenous across 99.9% of their genome (Falconer, 1981). The lines were tested for the presence of an *Accord* element in the *Cyp6g1* gene to diagnose DDT resistance (McCart *et al.*, 2005) and for the presence of *Wolbachia* (Champion de Crespigny & Wedell, 2006). Thirty-eight lines were found to be *Wolbachia* free and DDT resistant, and a subset of these lines were used in this study because both DDT resistance and *Wolbachia* infections influence sexual fitness (McCart *et al.*, 2005; Champion de Crespigny & Wedell, 2006) and because we could not test all isolines for logistical reasons. Flies were maintained in vials ¼ full of standard oatmeal-sugar-yeast-agar *Drosophila* medium, under a 12:12 L:D cycle at 25 °C.

A pilot study was carried out to test for an effect of cold-shock on female fitness. Cold-shocking vials (4 °C) of *D. melanogaster* for 15 min everyday for 10 days during development was found to significantly reduce the number of offspring emerging from eggs laid in the week after a single mating (which correlates with lifetime reproductive success (LRS) in *Drosophila* as most eggs are laid soon after copulation (e.g. Peng *et al.*, 2005; Taylor *et al.*, 2008)) by females exposed to cold (mean offspring produced (± SE) cold-shock = 29.4 ± 4; normal = 61.7 ± 11; $F_{1,20} = 4.47$; $P = 0.047$). This result is also consistent with previous findings (Murphy *et al.*, 1983; Watson & Hoffmann, 1996). Therefore, cold-shocking altered female reproductive value as all stressors should: stress acts as an energy drain taking resources away from reproduction (fitness) (Parsons, 2005). This indicates that the environmental manipulation was effective and environments probably differed in attributes other than just temperature.

Fifteen iso-female lines were randomly selected from those found to be *Wolbachia* free and DDT resistant. Nine of these were used to supply experimental females (female genotypes = female isolines), and the remaining six were used to provide experimental males (male genotypes = male isolines). Experimental males were propagated by moving male isolines to new vials every 2 days. Upon emergence, virgin males were collected twice a day. Males were housed with a maximum of 20 other males from the same male isoline for 3.5 ± 1 days to allow sexual maturation (Pitnick *et al.*, 1995).

To generate experimental females, four females and four males from each female isoline were paired and housed together and allowed to reproduce in individual vials for 24 h, before being moved to new vials for an additional 24 h of oviposition (= 8 vials per lines). Four vials from each isoline were placed under cold-shock (4 °C) for 15 min everyday for 10 days during development, commencing the day after oviposition. The other four vials were maintained under normal conditions (25 °C) throughout larval development. Any adults that emerged before 10 days were discarded, but note that peak emergence (i.e. when >85% of flies emerge) for both treatment occurred after this time. Virgin females emerging after 10 days were collected twice a day and housed with up to 20 females from the same line and treatment for 5 days to mature [4 days is sufficient for full maturity (Pitnick *et al.*, 1995)]. On day 5, females

were moved to individual vials and allowed to acclimatize for 1 h in a temperature-controlled room (25 °C). They were then placed with a male from one of the six male isolines in a fully factorial design.

We measured female preference in two ways. Firstly, we recorded whether the pair mated within 4 h of introduction (mate acceptance). This measure of preference has been used in a number of *Drosophila* studies (e.g. Chenoweth & Blows, 2005; McGuigan *et al.*, 2008). Secondly, if a mating occurred, we measured the time from the introduction of the male until copulation occurred (latency to mating). Male *Drosophila* use a range of courtship behaviours that a female interrupts with her own acceptance or rejection signals (Speith, 1974), and as a result, females are expected to mate faster with more attractive males (Speith, 1974; Kyriacou & Hall, 1986; Ritchie *et al.*, 1999; Acebes *et al.*, 2003; Taylor *et al.*, 2007; Hosken *et al.*, 2008). Furthermore, previous studies have shown that latency is influenced by female genotype (Heisler, 1984; Casares *et al.*, 1992; Sharma *et al.*, 2010), and both measures (mate acceptance and latency to mating) are consistent with the definitions of female preference (Kirkpatrick, 1987; Jennions & Petrie, 1997; Widemo & Saether 1999; Kirkpatrick *et al.*, 2006). We again note that the use of no-choice trials is a standard way to assess preference. Because male attractiveness is a composite trait and we were primarily interested in preference rather than the trait(s) being preferred, we did not ascertain precisely which male trait(s) females preferred. Thus, our measures of preference are for *all* traits that confer attractiveness to a male (see Head *et al.*, 2005). Furthermore, it is important to note that knowing the precise trait(s) that are preferred is not an absolute requirement for understanding female preference (Bakker & Pomiankowski, 1995). So for all possible male–female genotype combinations we have data on the proportion of pairs that successfully mated and the latency to mating for pairs that successfully mated. This design generated 1914 experimental pairs (half cold-shocked and half normal females = 106 pairs/line/treatment) and of these 73% (n = 1390) successfully copulated. We note here that although our experiment was fully factorial (each female genotype was exposed to each male genotype), final sample sizes varied per combination as not all pairings resulted in mating for example (i.e. the design was not fully balanced), but this has no impact on the analyses or results.

Statistical analyses

We tested for GEIs for female preference in two ways. Firstly, because mate acceptance is binary (0 = unmated, 1 = mated), we used an ordinal logistic regression model to examine the effects of male genotype, female genotype, female rearing environment (cold-shocked vs. normal) and all their interactions on this measure of female preference. Secondly, we examined the above effects on latency to mating in pairs that copulated using a general linear mixed model (GLMM) where male and female genotype were included as random effects and female rearing environment as a fixed effect. Latency to mating was normalized using a Box–Cox power transformation [$(x + 0.0000001)^{0.32}$], but all figures are presented using raw data for ease of interpretation. For simplicity, we subsequently refer to latency and acceptance in combination as female preference. For logistic reasons, mate choice trials were performed over several blocks (different days). Therefore, in both models, we have included a blocking effect to account for this temporal variation. We have included block as a covariate in the models, rather than as a random or fixed effect, because our aim was simply to statistically remove this variation not to explain it. Consequently, even though block was significant in our analysis of latency to mating, we only interpret the main effects and their interactions in this model. Both analyses were performed using the statistical package JMP (version 7.0, SAS, Cary, NC, USA), and data are presented as the mean ± 1 SE.

We determined whether the rank order of preference of the different female genotypes changed with rearing environment [i.e. an ecological crossover (Greenfield & Rodriguez, 2004)] using a randomization test in POPTOOLS (version 3.0), where we randomly shuffled the rank order of preference across female genotypes in the good environment (no cold-shock) treatment to obtain an expected distribution when there is no correlation between the rank order of genotypes across female rearing environments. Probabilities are the number of randomizations (out of 10 000) in which the pseudo-correlation (based on shuffled data) was equal to or greater than the actual correlation.

We also estimated the heritability of preference for females in both environments, as well as the genetic correlation of preference across these conditions. We estimated heritability from our inbred (iso-female) lines by calculating the coefficient of intraclass correlation (t) (Hoffmann & Parsons, 1988; David *et al.*, 2005) as:

$$t = \frac{nV_b - V_w}{nV_b + (n-1)V_w}$$

where n is the number of lines and V_b and V_w are the between line and within line variance components, respectively, estimated directly from an ANOVA including line as the main effect. The standard error of the intraclass correlation [SE(t)] was calculated according to Becker (1984) as:

$$\mathrm{SE}(t) = \sqrt{\frac{2(1-t)^2[1+(k-1)t]^2}{k(k-1)(n-1)}}$$

where k is the number of individuals sampled within each line. The heritability (h^2) of each phenotypic trait was then estimated according to Hoffmann & Parsons (1988) as:

$$h^2 = \frac{2}{\left(\frac{1}{t} - 0.5\right)}$$

The standard error of this estimate, $SE(h^2)$, was calculated according to Hoffmann & Parsons (1988) as:

$$SE(h^2) = \frac{2}{\left(1 - \frac{t}{2}\right)^2} SE(t)$$

This estimate accurately approximates narrow sense heritability, especially when dominance variance is negligible (Hoffmann & Parsons, 1988). However, even if there is substantial dominance variance in female preference, and while acknowledging that estimating heritabilities from iso-female lines is best carried out soon after line establishment (Hoffmann & Parsons, 1988), note that here we are only interested in showing that there is genetic variation in preference and that this differs (or not) with female rearing environment.

Genetic correlations (and their standard errors) across the two environments were estimated using the jackknife method of Roff and Preziosi (1994). In short, this procedure first estimates the genetic correlation between two traits using mean estimates for each line. A sequence of N pseudo-values is then computed by dropping each of the lines in turn and estimating the resulting correlations and using the formula:

$$S_{N,i} = Nr_N - (N-1)r_{N-1,i}$$

where $S_{N,i}$ is the ith pseudo-value, r_N is the genetic correlation estimated using the means of all N inbred lines and $r_{N-1,i}$ is the genetic correlation obtained by dropping the ith inbred line alone (Roff & Preziosi, 1994). The jackknife estimate of the genetic correlation (r_j) is then simply the mean of the pseudo-values, and an estimate of the standard error (SE) is given by:

$$SE = \frac{\sum_{i=1}^{i=N} (S_{N,i} - r_j)^2}{N(N-1)}$$

Using simulation models, Roff & Preziosi (1994) showed that this jackknife approach provides better genetic estimates than those based on conventional inbred line means when the number of inbred lines contained in the analysis is small (<20 lines). It is important to note that the estimates of genetic (co)variance from inbred lines contains variance because of dominance and/or epistasis and therefore should be considered broad-sense estimates (Falconer & Mackay, 1996).

Results

There was a significant effect of female genotype on both measures of female preference, indicating that this behaviour has a genetic basis (as previously reported for this (Heisler, 1984) and other species (e.g. Moore, 1989) (Table 1, Fig. 1), and heritability estimates of preference were substantial. Our manipulation of female developmental environment did not affect the average female preference (choosiness or acceptance), but altered its variance (Fig. 1 and see errors on heritability estimates below). However, there was a significant interaction between female genotype and environment – that is, the choosiness of a given female genotype depended on whether females were reared in good or cold environments, and there was strong concordance in the overall patterns shown by the two preference measures (Table 1, Fig. 1). This interaction is a GEI for female preference (Hunt *et al.*, 2004), and furthermore, this female–environment interaction shows variation in mate acceptance and latency is not because of male only effects (i.e. our measures of preference really were capturing information on female mate-choice behaviour and not only male courtship/harassment differences which would appear in the analyses as male effects) – confirming previous work on this species (e.g. Casares *et al.*, 1992). For both measures of female preference, heritabilities were substantially reduced under cold-shock (Heritability of mate acceptance: cold-shock = 0.58 ± 0.12, good conditions = 0.86 ± 0.06, $t = 4.42$, $P = 0.002$. Heritability of latency to mate: cold-shock = 0.83 ± 0.05, good conditions = 0.94 ± 0.03, $t = 2.85$, $P = 0.02$). There was also evidence of significant ecological crossovers (Greenfield & Rodriguez, 2004) in both measures of preference when females were in good and poor condition (Fig. 1), so that some female genotypes were more choosy (for example) when in good compared to bad condition, whereas the reverse was true for other genotypes. This is seen when comparing rank orders of both measures of female preference which were not significantly associated across female rearing conditions (Mate acceptance rank correlations across environments: $r = 0.52$, $P = 0.52$. Latency to mate rank correlations across environments: $r = 0.63$, $P = 0.07$). This rank order change in choosiness

Table 1 Male genotype, female genotype and the interaction between female genotype and condition influence the strength of female preference. Mate acceptance was analysed with an ordinal logistic regression. Latency to mating was Box–Cox transformed and analysed with a general linear mixed model. The overall results of either model do not change if the lower order interactions are removed by model simplification.

	Mate acceptance		Latency to mating	
	d.f.	Wald χ^2	d.f.	F
Block	1	55.60***	1,1281	98.27***
Female genotype (A)	8	43.49***	8,9.21	3.75*
Male genotype (B)	1	24.64***	5,5.07	50.26***
Environment (C)	1	1.10	1,5.83	0.84
A × B	8	7.50	40,39.99	1.48
A × C	8	31.77***	8,42.03	5.66***
B × C	1	0.31	5,41.27	0.18
A × B × C	8	12.79	40,1281	0.83

***$P < 0.0001$, *$P < 0.05$.

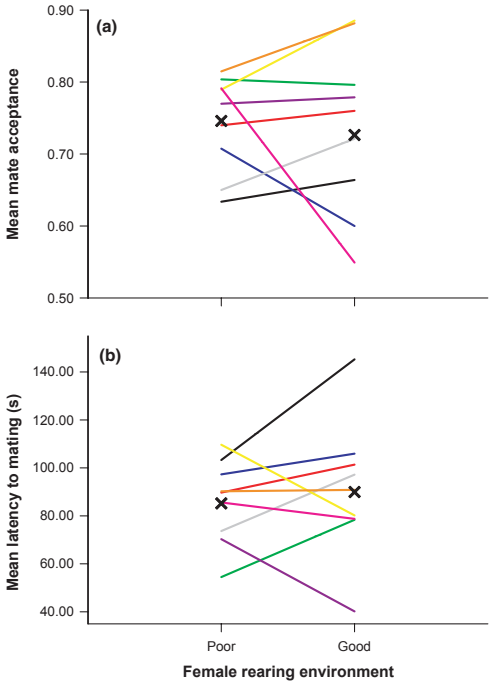

Fig. 1 The interaction between female genotype and environment influencing female preference, measured as (a) mate acceptance (% of pairs that mated) and (b) latency to mating. Each line represents the mean preference for one of each of nine female genotypes, with colours indicating the same female genotype in each plot. The crosses (X) mark overall means in each environment. Female environment was manipulated by cold-shock during development. For both forms of female preference, there is substantial genetic variation, although heritabilities for female preference are significantly reduced in the poor environment (see Results). Note that in b larger latency to mate values (= the *y*-axis) indicate less preferred and that there is a strong concordance in the overall pattern of the two preference measures (e.g. the variance always increases in the good environment, means do not greatly differ).

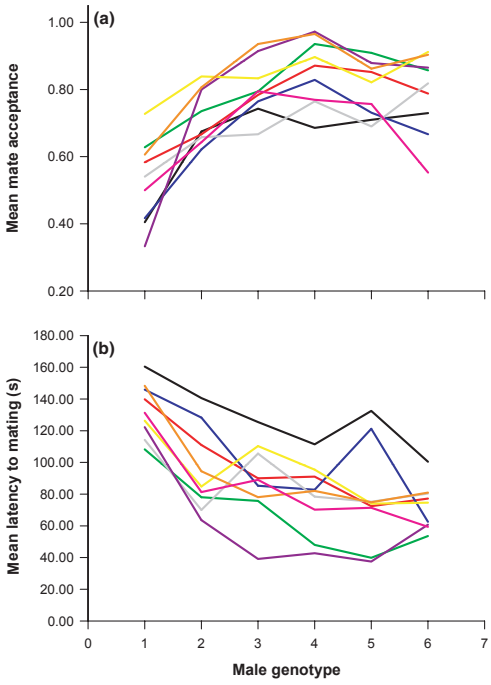

Fig. 2 The preference function describing the relationship between male genotype and female preference, measured as (a) mate acceptance and (b) latency to mating, for each female genotype. As can be clearly seen, some male genotypes (i.e. genotype 4) are more attractive than others (i.e. genotype 1) indicative of genetic variation in male attractiveness. There was no interaction between male and female genotype for either measure of preference (Table 1) demonstrating that on average, females agree on which males are attractive and which are unattractive. Note that in b larger latency to mate values (= the *y*-axis) indicate less preferred, and colours are used to indicate identical female genotypes in each plot.

is further illustrated by the comparatively weak genetic correlations across female rearing conditions (Fig. 1) with the genetic correlations between preference measures across female environments being low (Lande, 1980; Simmons & Ward, 1991) (Mate acceptance: $r_G = 0.40 \pm 0.09$. Latency to mate: $r_G = 0.51 \pm 0.03$). Consequently, the relative choosiness of female genotypes reared in a good environment did not always predict their relative choosiness when reared in a poor (cold-shock) environment (and *vice versa*). We also compared the environmental variance of both preference measures (the within isoline variances) across environments with paired *t*-tests and found that environmental variance in either preference measure did not vary across environments ($t < 0.55$; $P > 0.58$). This, in conjunction with the differences in genetic variance estimates, suggests that the phenotypic variance in preference differed across environments – this is because $V_P = V_G + V_E$ and while the environmental variances did not differ across environments, the genetic variances did.

There was a significant effect of male genotype on both components of female preference illustrating that females found, on average, some male genotype more attractive than others (Table 1, Fig. 2). This finding is consistent with male attractiveness having a genetic basis and confirms that the observed variance in female mate acceptance and latency to mate does not simply reflect differences in female receptivity. Consistent with this finding, there was no interaction between male and female genotype influencing preference (Table 1, Fig. 2), suggesting that although female preference depended on the interaction between female genotype and rearing environment, female genotypes on average agreed on the attractiveness rank of male genotypes (Fig. 2). This conclusion is further supported by nonsignificant interactions between male genotype and female rearing environment and between male genotype, female genotype and female rearing environment (Table 1).

Discussion

Our major finding is that there are GEIs for both measures of female preference, and there was very strong concordance in the pattern seen using either preference measure (see Fig. 1). Similar preference GEIs have also been reported for wax moths (Rodríguez & Greenfield, 2003). These GEIs provides a means of maintaining the genetic variation in female preference (Lewontin, 1955; Frank & Slatkin, 1990; Jia *et al.*, 2000) that is needed for preference to evolve, especially because the genetic variance in female preference differed across female environments, as did the rank order of both preference measures (Via & Lande, 1985). The change in genetic variance across environments also means that responses to direct selection on preference will vary across environments even if the strength of selection does not (Falconer, 1981). This additionally implies the magnitude of potential indirect benefits of choice could also vary across environments, because for example, daughters differentially inherit mothers' preferences and are more or less – depending on the environment – likely to mate with the type of males mothers chose as a result. If mothers were choosing males for good genes for example, daughters may be less likely to. However, GEIs for preference could represent adaptive plasticity (Rodríguez & Greenfield, 2003; Shuster & Wade, 2003) potentially negating these issues, although this has not been tested here. However, investigation of adaptive plasticity in wax moths found that the reaction norms for preference-thresholds in females do not seem to match the reaction norms for male signals, which suggests preference GEIs are not adaptive in that system (Rodríguez & Greenfield, 2003). Nonetheless, the environmental manipulation we used (cold-shock) will be frequently encountered in nature, making adaptive plasticity (in mate preference) a possibility (Shuster & Wade, 2003).

Perhaps more importantly, because genetic variance in female preference depended on female rearing environment, the strength of any genetic correlation between female preference and male attractiveness is also likely to vary across environments. This is because the strength of this genetic correlation depends on the product of the genetic variation of each character and how effective preference and attractiveness are at generating assortative mating (Bakker & Pomiankowski, 1995; also see Agrawal & Stinchcombe, 2009). Changes in the strength of this genetic correlation seem additionally likely if there are GEIs for male attractiveness traits (e.g. Jia *et al.*, 2000), which there inevitably seem to be whenever investigators look for them (Bussière *et al.*, 2008). The strength of this genetic covariance is critical in determining the evolutionary trajectories of preference and attractiveness traits (Lande, 1981; Arnold, 1983). For example, if the correlation is sufficiently strong – and the strength of sexual selection on male attractiveness-characters is large relative to natural selection and direct selection on preference is relatively weak – runaway evolution is predicted to occur (Lande, 1981; Arnold, 1983). Determining if and how the strength of this association varies across environments will be important to our understanding of the co-evolutionary dynamics of female mating preferences and the male sexual trait(s) they target, and hence sexual selection and the evolution of sexual fitness. However, we should also note that because females tended to agree on male attractiveness, any genetic correlation between preference and male traits could be relatively weak, although this inference should be tempered by the limited phenotypic space we sampled with the isolines.

We also found evidence that male attractiveness has a heritable basis as reported for *Drosophila* previously (e.g. Hoffmann, 1999; Taylor *et al.*, 2007), and in spite of GEI's for preference, female genotypes tended to generally agree which males were most attractive, although there was genetic variation for preference. Our preference heritabilities were high, ranging from 0.6 to 0.9. However, as explained above (Methods), estimating heritabilities from isolines is best carried out soon after line establishment (Hoffmann & Parsons, 1988) and all we wanted to do here was to estimate the *relative* genetic variances. Nevertheless, heritable female preference has been documented in *D. melanogaster* and other species previously (e.g. Heisler, 1984; Moore, 1989; Sharma *et al.*, 2010; reviewed in Bakker & Pomiankowski, 1995).

There are several other potentially important consequences of our findings we wish to highlight. First, when females were reared under good conditions, there was increased phenotypic variance in our measures of female preference, as estimated via the genetic and environmental variances. This potentially alters the strength of sexual selection on males, as the variance in male reproductive success could either increase or decrease with greater variance in female choosiness depending on how matings are redistributed among males. Thus, despite average preference not changing with female rearing environment, the strength of sexual selection on male attractiveness could. Therefore, even with identical genetic variation in male attractiveness, the strength of sexual selection on males can potentially vary across populations, and this variation in female choosiness may help maintain variation in male traits, or at least slow its erosion (Via & Lande, 1985). Analogous findings have been reported for post-copulatory sexual selection in *D. melanogaster* where mean female sperm-store dimensions (= preference) determine the strength of sexual selection on sperm length (post-copulatory attractiveness) (Miller & Pitnick, 2002). Finally, like all GEIs, the interaction between female preference and rearing environment could potentially facilitate divergence between subdivided populations and hence contribute to speciation (Wade, 2000; also see Etges *et al.*, 2007). The importance of sexual selection as a potential driver of

speciation has only recently become fully appreciated (Lande, 1981; West-Eberhard, 1983; Schluter, 2000; Martin & Hosken, 2003; Gay *et al.*, 2009; Hosken *et al.*, 2009), and our findings here emphasize this further.

In summary, we provide evidence for GEIs in female mate preference, and document changes in the heritability of preference across female rearing environments. This influences responses to direct selection on preference and can potentially alter the strength of genetic correlations between female preference and male attractiveness, with fundamental implications for the evolutionary trajectories of both. We have also only manipulated a single environmental variable and concerted changes in several variables (as would be the norm in nature) may magnify or otherwise influence the GEI detected. Finally, it is unclear how common female preference GEIs are, but the potential importance of widespread genotype-by-environment interactions for female preference should not be underestimated.

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