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Reinvestigating good genes benefits of mate choice in *Drosophila simulans*

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Studies investigating the genetic benefits of female mate choice frequently find Fisherian benefits to choice, at the same time as detecting small or no good genes (viability) effects. This could be because sons trade-off viability for increased mating success and, accordingly, it has been suggested that good genes benefits should be investigated in daughters. However, good genes benefits via daughters could also be disrupted by intralocus sexual conflict. As a result, it is not clear when and if good genes benefits should accrue. We investigated potential good genes effects in *Drosophila simulans* using an isofemale line approach. We assessed the attractiveness of males in two different ways and then measured the longevity, as well as lifetime reproductive success, of their daughters. We also assessed potential direct benefits of female mate choice and good genes effects through the longevity of sons. We found no evidence of direct or good genes benefits to females mating with attractive males, and the failure to find good genes effects via daughters was apparently not a result of masking through intralocus sexual conflict. The results obtained in the present study are consistent with previous findings in this species, and suggest that good genes benefits are at best very small in our study population. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, **106**, 295–306.

ADDITIONAL KEYWORDS: Diptera – indirect benefits – sexual selection.

INTRODUCTION

The benefits of female mate choice are the subject of much debate (Andersson, 1994; Andersson & Simmons, 2006; Hosken & House, 2011). Direct benefits of choice should be larger than indirect effects (Kirkpatrick, 1996; Kirkpatrick & Barton, 1997) and meta-analyses appear to confirm this (Møller & Alatalo, 1999; Jennions, Møller & Petrie, 2001; Møller & Jennions, 2001). Nevertheless, females may still gain indirect (genetic) benefits through their choice of mates (Andersson, 1994; Jennions & Petrie, 2000). These could be obtained in two general ways. First, by mating with attractive males, females could produce attractive sons and enjoy fitness benefits via the elevated mating success of sons (Fisherian benefits: Fisher, 1930; Lande, 1981; Kirkpatrick, 1985). Second, attractive males could be signalling their superior viability and, hence, by mating with them, females could produce high viability offspring (good genes benefits: Andersson, 1994; Jennions & Petrie, 2000).

Good genes benefits of mate choice were initially formulated as viability benefits (Lande, 1981; Arnold, 1983). However, there has been a tendency to include characters other than viability under a good genes umbrella more recently, with a number of studies reporting that mating with attractive males can enhance a range of offspring fitness components (Partridge, 1980; Boake, 1985; Norris, 1993; Petrie, 1994; Sheldon *et al*., 1997; Welch, Semlitsch & Gerhardt, 1998; Møller & Alatalo, 1999; Wedell & Tregenza, 1999; Brooks, 2000; Hine *et al*., 2002; Evans *et al*., 2004). It has also been argued that good genes effects are inevitable, with all indirect benefits ultimately becoming linked to good genes (Rowe & Houle, 1996; Jennions & Petrie, 2000). However, this apparently ignores the Fisher process, which can drag sexual traits well beyond their naturally selected optima (Shuster & Wade, 2003).

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It has also been suggested that allocation decisions could mask good genes benefits (Getty, 2002). For example, sons may trade-off viability with reproductive success (Pitnick & Markow, 1994; Droney, 1998; Kokko, 2001; Getty, 2002). This could then mask viability benefits obtained via sons, and bias conclusions about good genes (Kokko *et al*., 2002, 2003; Cameron, Day & Rowe, 2003; Hunt *et al*., 2004b). As a result, it has been suggested that good genes benefits should be investigated in daughters (Jennions & Petrie, 2000; Hunt *et al*., 2004b). However, there is a growing body of evidence that intralocus sexual conflict could further complicate potential good genes benefits. Intralocus conflict occurs when the genes that make good females make poor males, and vice versa (Rice & Chippindale, 2001), and negative intersexual fitness associations (i.e. the hallmark of this conflict) have been documented in a range of taxa (Rice, 1984; Norris, 1993; Fedorka & Mousseau, 2004; Pischedda & Chippindale, 2006; Foerster *et al*., 2007; Oneal, Connallon & Knowles, 2007; Harano *et al*., 2010) Additionally, intralocus conflict may be much more difficult to resolve than currently assumed (Day & Bonduriansky, 2004; Harano *et al*., 2010), potentially limiting good genes benefits through daughters. Furthermore, sexual selection driven by interlocus conflict may also preclude the enhancement of offspring viability (Arnqvist & Rowe, 1995; Hosken *et al*., 2009).

In the present study, we investigated potential good genes benefits of mating with attractive males in *Drosophila simulans*. Previous work has documented genetic variation for female mate preference (Sharma, Tregenza & Hosken, 2010), and also shown that male attractiveness is heritable and positively genetically correlated with sperm competitiveness (Taylor, Wedell & Hosken, 2007; Hosken *et al*., 2008). Additionally, females apparently gain no direct benefits from mating with attractive males (Taylor, Wedell & Hosken, 2008a; Taylor *et al*., 2008b). Although good genes benefits have been reported in several *Drosophila* species (*Drosophila melanogaster*: Partridge, 1980; Taylor, Pereda & Ferrari, 1987); *Drosophila montana*: Hoikkala, Aspi & Suvanto, 1998; *Drosophila serrata*: Hine *et al*., 2002), there is currently no evidence for this in our study population of *D. simulans*. Taylor, Wedell & Hosken (2010) used mating latency as an indicator of female preference (and hence male attractiveness) and then assessed the relationship between sire attractiveness and fitness of daughters. Their approach involved phenotypic parent–daughter associations and family-level associations, and they also tested for any direct effects of attractive males on female fitness. Their results suggested that females did not receive any indirect benefits of mate choice via fitness of daughters and that there were no direct effects of mate choice on female productivity (see Taylor *et al*., 2010). This is not to say good genes benefits do not exist but only that they have not been detected. This is perhaps not unexpected for the reasons outlined above, although good genes benefits also tend to be small (Møller & Alatalo, 1999), making them difficult to detect. Additionally, multiple independent tests should ideally be conducted to verify the validity of negative results (Palmer, 2000), and the use of diverse techniques is an appropriate way of doing this. Thus, additional investigations of good genes in *D. simulans* are warranted because the lack of evidence does not mean the phenomenon does not occur. With this in mind, we further investigated good genes in this fly and employed two new approaches using isofemale lines. This also allowed us to again assess potential direct benefits. Despite this new approach, we failed to find evidence for good genes or for direct benefits in our study population.

MATERIAL AND METHODS

The stock populations of *D. simulans* used here were collected from a wild population at Tuncurry, Eastern Australia in March, 2004 (20 wild caught isofemale lines). These had been mixed and maintained in large population cages (approximately 800–1000 flies/cage) with overlapping generations and free mate choice/mate competition from 2005. This stock has been used in a large number of investigations and harbours considerable phenotypic and genetic variation in all characters that have been assessed (Taylor *et al*., 2007; Hosken *et al*., 2008; Wright, Tregenza & Hosken, 2008; Sharma *et al*., 2010; Okada *et al*., 2011). We also maintained six isofemale lines from the original Australian collection (isolines 1–6), and established two additional isolines from the stock population (isolines 7 and 8). Both sets of isolines had been maintained in the laboratory for at least 3 years before the start of the present study. After several generations of within-line matings, these isolines are expected to be genetically homogenous within lines (i.e. they are approximate clones; for a full discussion of isoline uses, see Hoffmann & Parsons, 1988; David *et al*., 2005). All flies were reared on '*Drosophila* quick mix medium' (supplied by Blades Biological) under a 12 : 12 h light/dark cycle at 25 °C. Flies to be used in mating and fitness assays were initially collected as virgins from stock population laying vials or from cleared isoline vials. Briefly, egg-laying pots were left in the population cages overnight and then removed and incubated as above (12 : 12 h light/dark cycle at 25 °C). Virgin flies emerging from these egg-laying vials were separated and housed by sex (less than 10 flies per vial) within 8 h of eclosion with an excess of

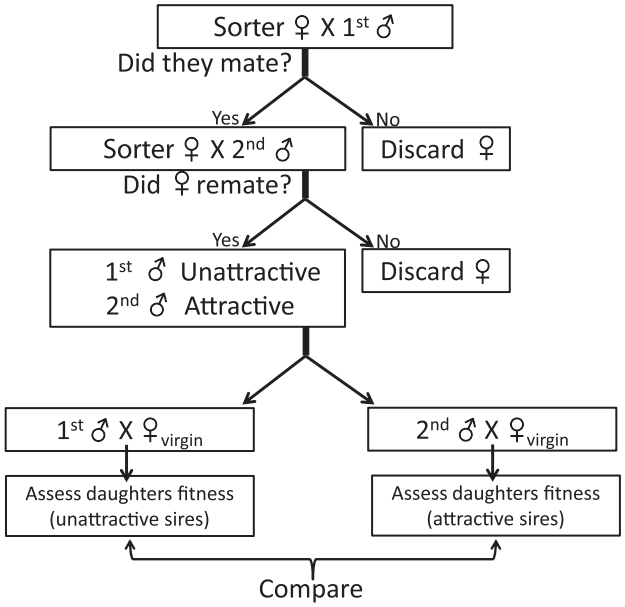

Figure 1. Flowchart depicting the experimental procedure in the first assay. A sorter female was mated with a virgin male and given the possibility to remate with another virgin male the next day. If she remated, the first male was classed as unattractive and the second one as attractive. Both males were then mated with virgin females from the same isoline as the sorter female. Subsequently, the fitness of daughters sired by attractive or unattractive males was assessed and the fitness scores were compared in a pairwise design.

the culture medium for 3 days (to ensure sexual maturity) before experiments.

We used two different approaches to assess potential good genes benefits. For our initial approach we employed the two stock population derived isolines (isolines 7 and 8) and used female remating behaviour as an indicator of male attractiveness. Subsequently, offspring fitness for attractive and unattractive sires was assessed (Fig. 1). Second, we used a panel of our six original isolines (isolines 1–6) and ranked them for the attractiveness of their males, successively assessing offspring fitness of the two most and two least attractive lines. Although 6 isolines may appear to represent a relatively small fraction of the total phenotypic space a fly population might occupy, a simple simulation reveals that this approach will capture most of the variation in the population. Assuming trait values in the source population were normally distributed and individuals (lines) are randomly sampled from this distribution, we drew six samples from a normal distribution with a mean of 16 and an SD of 5. We repeated this process 1000 times to generate a mean range of values that six samples generate. This mean range is 12.7. Comparing this range with 1000 values randomly drawn from the same normal distribution reveals that 80% of values fall within the range of 12.7 with a mean value of 16 ± 6.35, demonstrating that a sample of six individuals from a normally distributed population will typically capture 80% of the range of variation in that population along any given axis. Thus, the six isolines we use in the present study are likely to provide a reasonable sample of trait values and effects in the underlying population at large (assuming it too has trait values normally distributed) (also see David *et al*., 2005).

In our initial assessment of potential good genes benefits, we used isoline females to assess a male attractiveness in a stock population based on the isoline females' remating decision. Our rationale was that, when given a choice to remate, females would only remate with a more attractive male (i.e. trade-up) and, if there were good genes benefits to mate choice, we would be able to detect them in a pairwise comparison of the two males that mated with the female. Female remating decisions have previously been used as a measure of male attractiveness (Ivy & Sakaluk, 2007; Stewart *et al*., 2008), and although females of many *Drosophila* species mate readily, female *D. simulans* are fairly reluctant to remate (Taylor *et al*., 2008b), so this procedure appears to be appropriate (and has been used with *D. melanogaster*; Stewart *et al*., 2008). Additionally, previous attempts to detect good genes effects may have been made somewhat more difficult when female choosiness and male quality vary. For example, if females have different preference functions and also different levels of choosiness, it could be more difficult to definitively assign male attractiveness scores. This is alleviated by using isolines. Isolines can be considered to approximate clones and there is less variation in preference between pairs of females within isolines than between pairs of unrelated females (Sharma *et al*., 2010), making a 'relative' assessment of male attractiveness by the experimenters less prone to error when isolines are employed in attractiveness assessment.

For the assessment of potential good genes benefits, we paired a 3-day old stock-population male with a virgin female from one of two isolines (isolines 7 and 8) and observed the pairs for 3 h. Note that all matings took place between 09.00 h and 12.00 h (= the first 3 h of lights on), which corresponds with the period of peak mating activity in natural populations (Gromko & Markow, 1993), and this protocol was used throughout the present study unless stated otherwise. The mated pairs were then separated into individual vials soon after mating ended. The next day, each of the mated females was offered another 3-day-old virgin (stock-population) male and observed

for 3 h. If the female remated, the new mate was classed as attractive and her previous mate was deemed unattractive. These attractive or unattractive males were then mated with new virgin females after a gap of 1 day (from the same isoline as the initial female) and the fitness of subsequent daughters was assessed. This was necessary because we could not differentiate between sires in offspring from the initial female. However, because we use the same isolines, the genetic background of females is standardized.

Briefly, attractive and unattractive males were paired with virgin females and allowed to interact for 48 h. After 48 h, vials were checked for egg-laying, pairs were then removed, and vials were incubated. Virgin offspring emerging from these vials were collected as described above. For each sire, we selected multiple daughters at random and assayed them for fitness; approximately half were mated with a 3-day-old virgin stock-population male, to measure lifetime reproductive success (LRS), and the other half kept as virgins to assess longevity. In total, we assayed 466 and 554 daughters for the LRS and longevity assays. Daughters were 3–4 days old (sexually mature) when paired with a stock-population virgin male (of the same age) for 48 h. During this period, pairs were transferred to fresh vials with the culture medium every 24 h (twice), and then, after removing the males, females were moved to the final egg laying vial for 5 days. The LRS of each daughter was subsequently scored as the total number of offspring emerging from these three vials. Offspring from each vial were counted on the eighth day after the first eclosion (*D. simulans* larvae take 8–9 days to develop and eclose, so that 7 days of eclosing excludes any overlap with possible grandchildren). Taylor *et al.* (2008a) have previously shown this to be a good proxy for lifetime productivity from a single copulation. Note that it is this proxy of lifetime productivity that we refer to as LRS throughout the present study.

For the longevity assay, virgin daughters were housed at a density of three flies per vial and transferred to fresh vials once per week until death. These vials were checked daily for mortality and longevity was scored in days after eclosion. Throughout the present study, viability was measured as adult longevity because only viable embryos survive to adulthood, and adult longevity is a measure of adult viability. We used wing length as a measure of body size (Gilchrist & Partridge, 1999) to determine any association between body size and LRS or longevity. Wing length was measured *sensu* Sharma *et al.* (2011). Analyses were based on sire family means ($N = 46$ attractive, $N = 46$ unattractive) and comparisons were conducted pairwise because the attractiveness of males was relative to the other male that the initial female was exposed to.

For our second assessment, virgin males from six isolines were housed individually in separate vials and the next morning a female (from one of the same six isolines) was added to each male vial in a fully factorial manner (= 36 pair combinations). Each combination was replicated ten times (360 pairs). Pairs were continuously observed for 3 h, or until the start of mating. Previous work in this population has shown that approximately 95% of females mate during this time (Taylor *et al.*, 2008a). The time of female introduction and the start of copulation were recorded. We measured the time it took for a female to copulate with a male as our indicator of male attractiveness (mating latency: time from introduction of female to mating). This correlates with time from first courtship to mating but it is easier to measure (Taylor *et al.*, 2008a). Male *Drosophila* use a range of courtship behaviours that a female interrupts with her own acceptance or rejection signals (Spieth, 1974) and, as a result, females are expected to mate faster with more attractive males (Spieth, 1974; Kyriacou & Hall, 1986; Ritchie, Halsey & Gleason, 1999; Acebes, Cobb & Ferveur, 2003; Taylor *et al.*, 2007; Hosken *et al.*, 2008). Females also use a range of behaviours to reject unwanted male mating attempts, including ovipositor extension (which makes intromission impossible) and kicking (Spieth, 1974), and so it appears that males cannot force copulations with non-teneral females (Markow, 2000). Furthermore, previous studies have shown that latency is influenced by both male and female genotypes (Heisler, 1984; Casares *et al.*, 1992; Sharma *et al.*, 2010). We therefore reasoned that females should copulate faster with more attractive males, and latency has been widely used as a standard measure of female preference and therefore male attractiveness in *Drosophila* (Spieth, 1974; Ritchie *et al.*, 1999; Acebes *et al.*, 2003). Additionally, measuring attractiveness in this way excludes the potential for male–male competition interfering with our assessment of attractiveness, and this approach is widely used in behavioural studies (Houde & Torio, 1992; Gowaty, Steinichen & Anderson, 2002; Shackleton, Jennions & Hunt, 2005). The mean mating latencies thus obtained would show how attractive each genotype was judged (on average) by females from all isolines (Fig. 2). Based on this assessment, two attractive and two unattractive male lines were identified (Fig. 2), and new virgin males from these lines were then mated with stock females and used for assessment of the viability of daughters.

To conduct the assessment of the viability of daughters, males from the two most attractive (lines 1 and 2) and two most unattractive (lines 5 and 6) lines

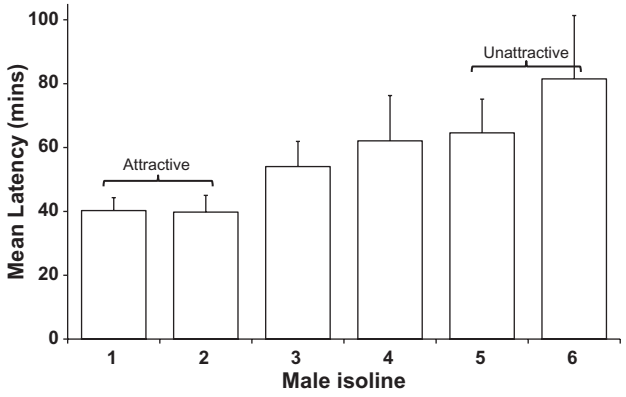

Figure 2. Mean ± SE male attractiveness for six *Drosophila simulans* isofemale lines. Attractiveness is shown as untransformed mating latency (means for 60 males per line). Lines 1 and 2 were considered as attractive (females mated fast with these males), whereas lines 5 and 6 were classed as unattractive (females took longer to mate with these males). Mating latency of attractive lines was significantly different from that of unattractive lines ($P < 0.01$).

were paired with a virgin stock population female (= outbred population-cage female) and observed as above ($N = 50$ per line = 200 males). Mating latency was recorded and we initially assessed the congruence between the attractiveness score generated from isoline females and the assessment of stock-population females. Both the Kruskal–Wallis and median tests confirmed that latency of males judged to be most attractive by isoline females were also judged to be more attractive by stock-population females (Kruskal–Wallis $\chi^2 = 4.09$, d.f. = 1, $p = 0.04$; median $\chi^2 = 5.78$, d.f. = 1, $p = 0.024$; mean latency attractive: 73.45 ± 5.74; mean latency unattractive: 94.23 ± 5.74). This suggests that the stock-population females were in agreement with the assessment of relative male attractiveness by isoline-females, which further supports our claim that the isolines are providing an accurate picture of the population as a whole.

After a single copulation with stock-population females, males were removed and stored for future measurements. Females (dams) were left to lay eggs for 24 h, after which they were transferred to a new egg laying vial for another 24 h. They were then moved into a final vial where they laid eggs for a further 5 days. LRS of these dams was scored as described previously. Two virgin daughters from each dam were collected from these vials, housed alone, and transferred to fresh food vials once per week until death to assess their adult longevity. This gave us a total of 400 daughters (= 100 daughters per isoline = 200 daughters of attractive males and 200 daughters of unattractive males). We also collected two sons from each dam and treated them as per the daughters to assess their longevity. This enabled us to test for an effect of sire attractiveness on the longevity of sons (with the caveats previously mentioned) and to regress mean daughter longevity against mean son longevity to determine whether any lack of sire-daughter associations were a result of negative intersexual correlations (Chippindale, Gibson & Rice, 2001). Although a negative relationship between sons and daughters longevity is expected under intralocus sexual conflict, it is worth noting that it may not always be indicative of intralocus conflict. Such a relationship may also indicate a higher investment in male sexual traits that are detrimental to survival (Kokko, 1997; Hunt *et al*., 2004a).

Statistical analysis

Data analysis was conducted using SPSS-PASW, version 18. Raw data were tested for normality using Shapiro–Wilks tests and $\log_{10}$- or square-root transformed to improve normality where appropriate. Nonparametric tests were used where normality assumptions of parametric tests could not be met. For the first experiment, our data did not meet assumptions of normality and we could not transform them in such a way to meet the assumptions of parametric tests. We therefore used Wilcoxon matched pairs signed-rank tests to assess the differences in the LRS and longevity of daughters sired by attractive or unattractive males (i.e. males were paired based on the common female used to judge their relative attractiveness). This dataset was additionally examined using generalized linear models (GLMs) with LRS or longevity as the dependent variable, and sire attractiveness and isoline as the predictors (with quasi-poisson error structure). A stepwise elimination approach was taken to obtain a minimal adequate model. Results from the GLM analyses are presented alongside those from the nonparametric tests used earlier. We also compared Kaplan–Meier survival curves (for the longevity data) with log-rank tests using the survdiff procedure in R, version 2.3.0 (R Development Core Team, Vienna, Austria). Note that our conclusions do not change, regardless of the statistical method applied. For the second experiment, we used a mixed model univariate analysis of variance (ANOVA), with longevity of daughters (dependent), sire attractiveness (fixed effect), and isoline nested within sire attractiveness (random effect), aiming to examine the effect of sire attractiveness on the longevity of daughters. The same model was applied to test the longevity of sons and we note here that our conclusions do not change if the predictors are treated as fixed or random effects. Although our

primary interest was the relationship between sire attractiveness and longevity of daughters, we also examined the direct effect of attractive males on female fitness (i.e. the direct benefits to dams from their mates) by using dams' LRS as the dependent variable and the same predictor variables (sire attractiveness and line within attractiveness). We additionally regressed mean (per sire family) longevity of daughters against the longevity of sons to assess intersexual longevity associations. Sample sizes vary across some analyses as a result of missing data.

RESULTS

The results of the first experiment where we used females' remating decision as a criteria to evaluate male attractiveness (using two-tailed *P*-values from related-samples Wilcoxon signed ranks tests) suggested no differences in the LRS ($mean_{Attractive}$ = 47.43 ± 0.56; $mean_{Unattractive}$ = 48.21 ± 0.61; $Z = -0.96$, $p = 0.34$) or longevity ($mean_{Attractive}$ = 45.99 ± 2.24; $mean_{Unattractive}$ = 44.10 ± 1.46; $Z = -0.80$, $p = 0.42$) of daughters sired by attractive or unattractive males. Body size could potentially influence this result (i.e. if daughters of unattractive males were larger than daughters of attractive males), although we could not include size as a covariate in the previous analysis. However, a paired *t*-test of the wing-length of daughters found no difference between the body size of daughters from attractive or unattractive sires ($mean_{Attractive}$ = 1.31 ± 0.005; $mean_{Unattractive}$ = 1.31 ± 0.004; $N = 38$, $t = -0.24$, $p = 0.81$), which suggests the lack of difference in LRS and longevity is not a result of size differences in daughters. Note that a paired *t*-test was used because the initial assignment of male attractiveness was based on a single female judging two males (i.e. data were paired). Reanalysis of this data set using GLM (see methods above) revealed no effect of sire attractiveness on either the LRS ($F_{1,89} = 0.46$, $p = 0.50$) or longevity ($F_{1,89} = 0.88$, $p = 0.35$) of daughters. Survival analysis of the longevity dataset revealed no differences between the survival curves for daughters of attractive and unattractive sires ($\chi^2_1 = 2$, $p = 0.157$).

Results from the mixed model ANOVA of experiment two using family means of longevity of daughters (dependent), sire attractiveness and sire line nested within attractiveness (as predictors) revealed no effect of sire attractiveness on the longevity of daughters (Table 1). However, we did see a significant line (within attractiveness) effect, which was driven by one attractive line producing long-lived daughters (Fig. 3, Table 1). Post-hoc pairwise comparisons of the line effect indicated that the mean for line 2 was significantly higher than that of all other lines (mean $difference_{L2–1}$ 8.34 ± 1.17, $_{L2–5}$ 7.99 ± 1.17, $_{L2–6}$ 8.75 ± 1.17; all $p < 0.001$), and none of the other lines differed from each other (all $p > 0.9$). We also analyzed these data by taking isoline means instead of family means for the longevity of daughters. This also revealed no difference in the longevity

Table 1. Analysis of variance for mixed model analysis using family means of longevity of daughters as the dependent variable and sire attractiveness and sire line nested within attractiveness as predictors

Source of variation	d.f.	Mean square	*F*	*p*
Attractiveness	1	882.00	1.01	0.42
Error	2	876.67		
Line (Attractiveness)	2	876.67	25.67	< 0.001
Error	196	34.16		

Note that there was no effect of sire attractiveness on the longevity of daughters but there was a significant line (within attractiveness) effect (for a visual representation, see Fig. 3).

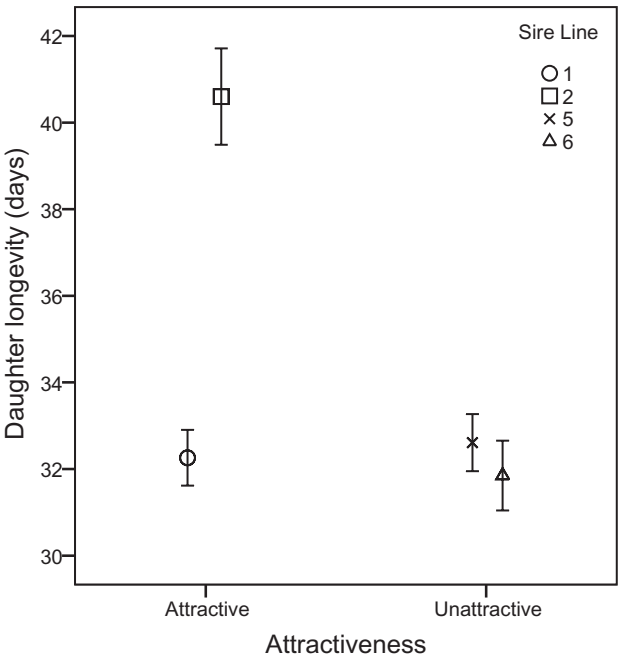

Figure 3. Interaction plot showing a significant isoline effect on the longevity of daughters. The longevity of one attractive line is between that of the two unattractive lines and daughters of line 2 males had increased longevity. There was no overall effect of male attractiveness. The *x*-axis represents male attractiveness and the *y*-axis represents the longevity of daughters (days). An open circle, square, cross, and triangle represent attractive (1, 2) and unattractive (5, 6) lines, respectively. Error bars represent the SE.

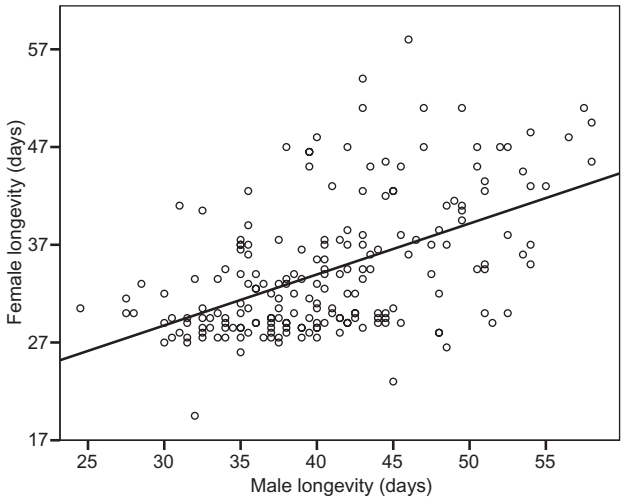

Figure 4. Regression of female and male offspring longevity from attractive and unattractive sires (R^2 linear = 0.27). This relationship was significant even when analyzed separately for offspring of attractive and unattractive sires. The data shown are untransformed and include information from the offspring of both types of sires.

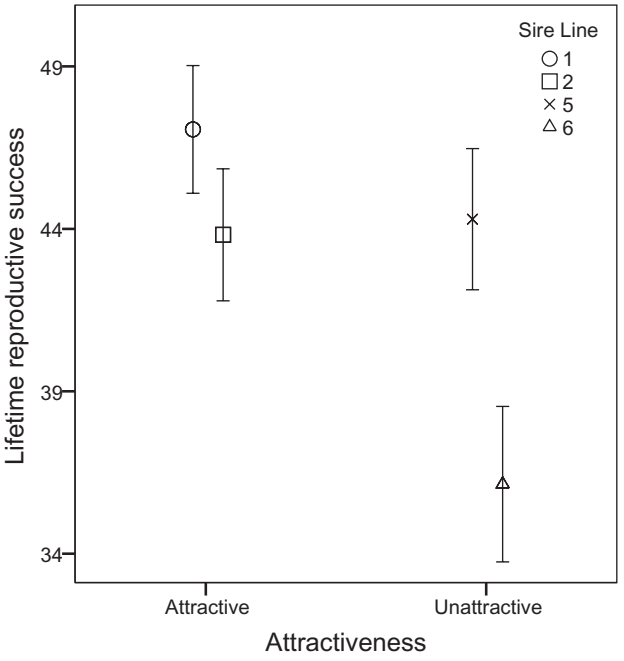

Figure 5. Interaction plot showing a significant isoline effect on dams' lifetime reproductive success. The *x*-axis represents male attractiveness and the *y*-axis represents the lifetime reproductive success of dams mated with attractive or unattractive sires. An open circle, square, cross, and triangle represent attractive (1, 2) and unattractive (5, 6) lines, respectively. Error bars represent the SE.

of daughters of attractive or unattractive lines (Kruskal–Wallis $\chi^2 = 0.6$, d.f. = 1, $p = 0.67$). We found similar results when assessing the longevity of sons, with no attractiveness effect ($F_{1,2} = 0.19$, $p = 0.70$) but, again, there was a line (within attractiveness) effect ($F_{2,196} = 62.88$, $p < 0.001$). This time, however, post-hoc pairwise comparisons revealed that one attractive line (line 2) significantly elevated longevity of sons relative to all other lines (mean difference_{L2-1} 11.72 ± 1.05, $_{L2-5}$ 9.26 ± 1.05, $_{L2-6}$ 7.7 ± 1.05; all $p < 0.001$), although the other attractive line (line 1) produced sons with longevity significantly lower than that of one unattractive line (line 6) (mean difference_{L1-6} -4.01 ± 1.05; $p = 0.001$). There were no other significant differences.

We also compared the longevity of sons and daughters to determine whether there were any indications of intralocus sexual conflict. We found that family mean longevity of daughters was positively related with family mean longevity of sons ($\beta = 0.52 \pm 0.06$, $F_{1,198} = 73.42$, $p < 0.001$, $R^2 = 0.27$; Fig. 4). This relationship remained positive and significant even when we split the data across attractive and unattractive sires ($\beta_{\text{Attractive}} = 0.49 \pm 0.08$, $F_{1,98} = 39.80$, $p < 0.001$, $R^2 = 0.29$; $\beta_{\text{Unattractive}} = 0.46 \pm 0.11$, $F_{1,98} = 16.78$, $p < 0.001$, $R^2 = 0.15$).

Assessment of the LRS of mothers revealed no direct benefits from mating with attractive males ($F_{1,2} = 1.45$, $p = 0.35$). However, there was again a significant line effect in the model ($F_{2,183} = 4.11$, $p = 0.02$; Fig. 5) and post-hoc pairwise comparisons revealed this was a result of Line 1 having significantly greater LRS than line 6 (mean difference_{L1-6} 10.92 ± 3.07; $p < 0.01$), although none of the other comparisons differed (all $p > 0.05$). This additionally indicates that larval viability did not favour more attractive males unless females laid more eggs for less attractive males, which is unlikely.

DISCUSSION

The primary aim of the present study was to test whether attractive males produced daughters with enhanced viability (measured as adult longevity), which would be consistent with good genes benefits of mate choice. We assessed the fitness of daughters because theory suggests sons may trade viability for mating success, and hence it is possible that good genes effects are only detectable via daughters (Kokko, 2001; Getty, 2002). We have previously shown that there is genetic and phenotypic variation in female preference (Taylor *et al.*, 2008a; Sharma *et al.*, 2010). However, although previous studies have

reported Fisherian benefits of mate choice in this species (Taylor *et al*., 2007; Hosken *et al*., 2008), evidence of good genes effects has not been documented (Taylor *et al*., 2010), even though these benefits have been considered inevitable (Jennions & Petrie, 2000).

In the present study, we assessed good genes benefits using two different approaches to assign male attractiveness. However, despite the protocols being different from those used in previous work (Taylor *et al*., 2010), we did not consistently detect evidence of good genes benefits of mate choice. Whilst our first assay did not provide any evidence for a good genes effect, our second assay showed that males from one attractive isoline sired long-lived daughters. Although this provides some evidence for a good genes effect, the results from our first assay and the lack of an overall male attractiveness effect, together with previous findings (Taylor *et al*., 2010), make us reticent to conclude that attractive males generally confer good genes benefits to female *D. simulans*. Additionally, the longevity of sons was not significantly influenced by sire attractiveness, although there are caveats to this assessment that we have previously discussed (see Rowe & Houle, 1996; Jennions & Petrie, 2000).

It is possible that the single isoline that enhanced the longevity of daughters (and sons) displayed relatively less inbreeding depression for this trait, perhaps through more purging, and this accounts for the line effect found in the present study. This could occur even though isolines had undergone the same theoretical levels of inbreeding because it is always possible that, by chance, some isolines contain fewer of the deleterious recessive alleles that appear to be generally responsible for inbreeding depression [i.e. the partial dominance hypothesis is widely accepted to be the cause of inbreeding depression (Charlesworth & Charlesworth, 1999)]. Furthermore, using different approaches, we have found substantial inbreeding effects on male and female fitness correlates in our study population (Wright *et al*., 2008; Okada *et al*., 2011), all of which is consistent with a differential inbreeding depression explanation for the single line effect. Alternatively, genetic compatibility could be involved (Tregenza & Wedell, 2000), with this isoline being more compatible with stock-population females, although this is less likely. However, whatever the cause of the line effect, we nevertheless failed to detect a male attractiveness effect (positive or negative) *per se* on the fitness of daughters (longevity or LRS). Our results therefore contrast with studies showing fathers' reproductive success negatively affecting the fitness of daughters (Fedorka & Mousseau, 2004; Pischedda & Chippindale, 2006; Foerster *et al*., 2007; Oneal *et al*., 2007), although they are consistent with other studies reporting neutral or weak effects of a father's reproductive success on the fitness of daughters (Norris, 1993; Jones, Quinnell & Balmford, 1998; Tomkins & Simmons, 1999; Rundle, Ödeen & Mooers, 2007; Maklakov & Arnqvist, 2009).

It is possible that we failed to detect a sire attractiveness/daughter fitness association because of the standardized and relatively benign laboratory conditions under which the assays were conducted (Qvarnström & Price, 2001; Hunt *et al*., 2004b; Schmoll *et al*., 2005). This is always a possibility but the same criticism can be made when assays take place under harsh conditions: differences are not detected because severe environments reduce phenotypic variation. Additionally, these are the same experimental conditions under which Fisherian benefits of mate choice were documented (Taylor *et al*., 2007), and the lack of any detectable good genes benefits is also consistent with previous findings (Taylor *et al*., 2008a, 2010).

In a meta-analysis of good genes benefits of mate choice, Møller & Alatalo (1999) found that effects sizes are usually small, and it is possible that our statistical power was simply not great enough, or that the phenotypic space covered by the isolines was small relative to total phenotypic space, obscuring associations. We acknowledge that the strength of our second experiment was relatively low and that future experiments could benefit from a design with a large number of isolines. However, our first experiment employed a large sample size (92 population cage males and more than 1000 daughters) and therefore had much greater power, and this together with previous work sampled a large proportion of phenotypic space, although both failed to detect any evidence of good genes (Taylor *et al*., 2010). Hunt *et al*. (2004b) stress that total fitness and breeding values should both be estimated to assess genetic quality accurately, and male attractiveness and mating success are the key determinants of male fitness, with a genetic basis (Taylor *et al*., 2007; Hosken *et al*., 2008), which is why they were employed in the present study. We also used two measures of potential good genes benefits: LRS and longevity (the latter of which is the benefit originally envisaged from good genes), and still found no compelling evidence of good genes benefits of mate choice.

One mechanism that could obscure good gene benefits through daughters is intralocus sexual conflict. Intralocus sexual conflict occurs when the gene combinations that produce a good male, produce a poor female, and negative (genetic) intersexual fitness correlations are considered to be signatures of this conflict (Rice & Chippindale, 2001). Intra-family correlations approximate genetic correlations, especially when the traits are measured in different groups

of individuals (Lynch & Walsh, 1998), as in the present study, and therefore the positive and significant intersexual association that we observe is not consistent with genes good for males being bad for females. A large number of studies have now provided evidence of intralocus sexual conflict in *Drosophila melanogaster* (Rice, 1984, 1992, 1998; Rice & Chippindale, 2001; Prasad *et al*., 2007), and Innocenti & Morrow (2010) suggested that intralocus sexual conflict can potentially neutralize any indirect genetic benefits of sexual selection, including good genes effects. However, our data are not consistent with intralocus conflict obscuring good genes because we found that the longevity of sons and daughters was positively correlated, and similar findings have also been reported for other insects (Hosken *et al*., 2003). Note that we are not suggesting an absence intralocus conflict in *D. simulans*, only that we currently have no clear evidence of sexual conflict over longevity.

We also found no direct benefits of male attractiveness but, again, we detected a significant line effect. The former finding is consistent with many previous assays (Taylor *et al*., 2008a, b) and contrasts with work on *D. melanogaster* (Pitnick & García-González, 2002; Friberg & Arnqvist, 2003). The effect on the LRS of mothers only occurred in one of the attractive lines and this is not the attractive line that elevated offspring longevity. Again, the reasons for this specific direct effect are not clear, although they could relate to differential inbreeding depression (see above) in male fertility (which would explain why line 6 sires fathered so few offspring compared to other lines, although only one post-hoc pairwise comparison was significant). Male fertility appears to be prone to inbreeding depression generally (Gage *et al*., 2006; Roldan & Gomendio, 2009; Michalczyk *et al*., 2010; Simmons, 2011), and in this population specifically (Okada *et al*., 2011). Inbreeding depression for male fertility as an explanation for this direct fitness effect is a possibility because we only counted offspring and not eggs. However, we note that, for a good genes viability effect to be missed by the adult viability assessment that we employed, dams of attractive males would have to lay relatively fewer eggs, which appears counterintuitive (but see also Gowaty, 2008). Nonetheless, this needs to be assessed. In any case, there does appear to be some male genetic variation that directly and indirectly influences female fitness, although this does not appear to be generally related to good genes benefits, and the most parsimonious explanation is differential inbreeding depression of the isolines.

The present study aimed specifically to test for good genes benefits of mate choice and we primarily assessed this via the longevity of daughters. The results obtained provide no evidence that females mating with attractive males generally obtain good genes benefits of mate choice, nor do they generally gain direct benefits. The lack of a sire-attractiveness/daughter-fitness association does not appear to the result of intralocus sexual conflict however, because family-level intersexual fitness correlations were positive and significant. The current evidence is consistent with an absence of good genes benefits of female mate choice in our population.

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