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Testing the correlated response hypothesis for the evolution and maintenance of male mating preferences in *Drosophila serrata*

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Abstract

Mate preferences are abundant throughout the animal kingdom with female preferences receiving the most empirical and theoretical attention. Although recent work has acknowledged the existence of male mate preferences, whether they have evolved and are maintained as a direct result of selection on males or indirectly as a genetically correlated response to selection for female choice remains an open question. Using the native Australian species *Drosophila serrata* in which mutual mate choice occurs for a suite of contact pheromones (cuticular hydrocarbons or CHCs), we empirically test key predictions of the correlated response hypothesis. First, within the context of a quantitative genetic breeding design, we estimated the degree to which the trait values favoured by male and female choice are similar both phenotypically and genetically. The direction of sexual selection on male and female CHCs differed statistically, and the trait combinations that maximized male and female mating success were not genetically correlated, suggesting that male and female preferences target genetically different signals. Second, despite detecting significant genetic variance in female preferences, we found no evidence for genetic variance in male preferences and, as a consequence, no detectable correlation between male and female mating preferences. Combined, these findings are inconsistent with the idea that male mate choice in *D. serrata* is simply a correlated response to female choice. Our results suggest that male and female preferences are genetically distinct traits in this species and may therefore have arisen via different evolutionary processes.

Introduction

Mate preferences are ubiquitous in nature, and it has long been recognized that the sexual selection they generate is responsible for a significant amount of the phenotypic diversity observed both within and among species (Andersson, 1994). Mate preferences are often seen as an important source of directional sexual selection within populations (Andersson, 1994) and estimates from the wild suggest sexual selection may often be stronger on average than natural selection (Hoekstra *et al.*, 2001; Kingsolver *et al.*, 2001; Hereford *et al.*, 2004). Female preferences have traditionally received the most attention due to the expectation that in the majority of sexual systems without parental care, only male fitness increases through quantity rather than quality of mates (Bateman, 1948; Andersson, 1994). More recent empirical and theoretical work acknowledges that male mate preferences may also be important, even in species with conventional sex roles and in which female preferences exist (Amundsen, 2000b; Bonduriansky, 2001; Clutton-Brock, 2007; Edward & Chapman, 2011). However, in systems without sex role reversal, it is not always clear if male mate choice exists due to direct selection for choosy males or as an indirect, genetically correlated response to female choice arising as a consequence of a genome that is largely

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shared between the sexes (Lande, 1980; Halliday & Arnold, 1987; Amundsen, 2000a,b; Kraaijeveld *et al.*, 2007).

Shared genetic variance for traits expressed in both sexes, but which are subject to sex-limited selection, will likely result in a correlated response in the unselected sex (Lande, 1980). With respect to mate preferences, the correlated response hypothesis predicts that males should favour similar traits to those preferred by females. Furthermore, due to the correlated evolution of mate preferences in males, females will ultimately express the trait that they target in males, leading to ornamented females (Amundsen, 2000b; Kraaijeveld *et al.*, 2007; Clutton-Brock, 2009). Thus, it is expected that an analysis of sexual selection would detect males and females preferring phenotypically and genetically correlated values of the same signal traits (Amundsen, 2000b; Kraaijeveld *et al.*, 2007; Clutton-Brock, 2009). A second prediction of the correlated response hypothesis is that there should be a positive genetic correlation between the sexes for the mating preferences themselves owing to their pleiotropic genetic basis (Amundsen, 2000b; Kraaijeveld *et al.*, 2007; Clutton-Brock, 2009; Edward & Chapman, 2011). The majority of previous work testing the correlated response hypothesis has focused on identifying differences in selection and testing for evidence of correlations between the sexes for the signal traits targeted by female mate choice (Amundsen, 2000b; Kraaijeveld *et al.*, 2007; Clutton-Brock, 2009; Tobias *et al.*, 2012). We aimed to test the key prediction of the correlated response hypothesis by estimating genetic variance in male and female mating preferences themselves and testing for the presence of a genetic correlation between the sexes. To our knowledge, the prediction of a strong genetic correlation between the sexes for mate preferences has yet to be tested, perhaps as a result of the empirical challenges inherent in the genetic analysis of mate preferences that result from the need for high statistical power (Chenoweth & McGuigan, 2010).

We use the Australian native *Drosophila serrata*, a species with mutual mate choice, to test whether male mate preferences are the result of a correlated response to selection for female mate choice. Mate preferences in male and female *D. serrata* both target a homologous suite of CHCs in the opposite sex. Male CHC displays have been shown to genetically covary with fitness (Delcourt *et al.*, 2012), and CHCs appear to indicate both male (Delcourt & Rundle, 2011; Gosden & Chenoweth, 2011) and female (Chenoweth *et al.*, 2007) condition. Although the genetic basis of CHCs is to some extent shared between the sexes (Chenoweth & Blows, 2003, 2005; Gosden *et al.*, 2012), the cross-sex genetic correlation for the specific combination preferred by each sex has not been previously estimated, nor has the cross-sex genetic correlation of mate preferences. Our approach involved conducting both male and female binomial choice mating trials, incorporated within a quantitative genetic breeding design, to: (i) test for differences in the strength and direction of phenotypic sexual selection in both males and females; (ii) estimate the genetic correlation between male and female- preferred CHC blends; and critically (iii) estimate the sex-specific genetic variances and cross-sex genetic correlation for mate preferences.

Materials and methods

We used a set of 51 inbred lines (IL) derived from wild-caught, inseminated females collected from The University of Queensland campus in St Lucia, Brisbane, Australia. The lines were created using repeated rounds of full-sib mating for a minimum of 15 generations. Inbreeding was initiated for approximately 100 lines, and the lost lines represent either the purging of highly deleterious recessive alleles or other random demographic effects that occur when maintaining such a small number matings per line. Inbreeding began immediately after collection, thereby minimizing any adaptation to the laboratory environment and helping maintain the natural allelic variation representative of the population from which they were founded. To avoid possible issues of inbreeding depression in our experimental assays, we randomly selected three of the inbred lines to act as reference lines. Males from these reference lines were separately crossed to females from the remaining 48 inbred lines, creating a population of 144 unique F_2 heterozygote genotypes that could easily be replicated.

Using the offspring from these IL crosses, we conducted standard two-stimulus binomial mating trials for both sexes, as outlined in Chenoweth & Blows (2005). In each trial, a single focal fly from an IL cross was randomly paired with two individuals of the opposite sex that had both been randomly taken from the F_2 offspring of the same set of 144 F_1 crosses. For each F_1 cross, we conducted 8 mating trials for each sex. To identify individuals designated as signallers during the trials, we clipped a small piece from the alternative wing of each fly, with an equal number of individuals clipped on each wing in all F_1 crosses. During a trial, once a mating was observed the competitor flies were removed, scored as either chosen or rejected, and their CHCs were extracted by hexane washing using established techniques (Blows & Allan, 1998). All flies used in the mating trials were collected as virgins and held separately by sex for a minimum of 6 days at 25°C with 12:12 h light/dark. Competitor flies were held four per vial, and focal flies were held individually as the mating trials were later performed in the same vial. Trials were performed across two blocks with all F_1 genotypes represented in each block.

The CHC profiles for the competing males and females were analysed via standard gas chromatogra-

phy (GC) methods for this species (Rundle *et al.*, 2008). The areas under eight chromatograph peaks of interest (5,9-$C_{24:2}$; 5,9-$C_{25:2}$; 9-$C_{25:1}$; Z-9-$C_{26:1}$; 2-Me-C_{26}, 5,9-$C_{27:2}$; 2-Me-C_{28}; 5,9-$C_{29:2}$) were integrated and then expressed as proportional values of the total CHC concentration of each individual to correct for technical error association with quantifying absolute abundances. Following past studies (Blows & Allan, 1998; Blows *et al.*, 2004), proportions were transformed into seven log-contrast values to permit multivariate statistical analyses following Aitchison (1986) and using 5,9- $C_{24:2}$ as the common divisor. The methylalkane 2-Me-C_{30}, which has been included in studies of *D. serrata* in the past, was uniformly higher in mated females from the male choice trials, resulting in a disproportionate effect on the variance explained in the male choice trials. Such a pattern has not been previously observed in this species and, because it was consistent with physical transfer during copulation or physiological changes induced by mating, this trait was excluded from our analyses. More detail on the statistical treatment of CHCs can be found in Blows & Allan (1998). For multivariate outlier detection and removal, we employed the Mahalanobis distance technique described in Sall *et al.* (2005) and implemented in the multivariate package of JMP version 8 (SAS Institute, Cary, NC, USA). We collected a total of 3992 GC samples, and after accounting for failed GC samples (33) and multivariate outliers (270), a total of 1888 male and 1801 female CHC profiles were available for subsequent analysis.

Statistical analyses

The principal aim of our study was to determine the degree to which male mate preferences have evolved and are maintained as a genetically correlated response to female mate preferences. To facilitate cross-sex comparisons, log-contrast CHC values were individually standardized to have a mean of zero and unitary variance prior to the statistical analyses. We chose to standardize in this manner as the traits of interest are log-transformed compositional data points (Aitchison, 1986), resulting in a difference scale that can only be meaningfully scaled by the variance (Hansen *et al.*, 2011; Houle *et al.*, 2011). All analyses were performed in SAS version 9.3 (SAS Institute).

We first tested for the presence of linear and non-linear sexual selection on the seven logcontrast CHCs for each sex separately. Following Fairbairn & Preziosi (1996), we used ordinary least squares multiple regression to estimate the selection gradients (Lande & Arnold, 1983) and a logistic regression model with a binomial probability distribution and logit link function to test their significance. We then tested for differences between the sexes in directional sexual selection using the sequential model-building approach outlined in Chenoweth *et al.* (2012). Briefly, we constructed a logistic regression model with a binomial probability distribution and logit link function that was fit via maximum likelihood. The model included all the interaction terms between each logcontrast CHC and sex giving:

$$M = \beta_0 + \alpha_0 \text{sex} + \sum_{i=1}^{n} \beta_i C_i + \sum_{i=1}^{n} \alpha_i C_i \text{sex} + \varepsilon. \qquad (1)$$

Here, M is the measure of binomial mating success, C_i is the logcontrast concentration of the ith CHC, $\alpha_0$sex is the intercept (accounting for sex differences in mating success) and $\alpha_i C_i$sex is the interaction between the selection gradients (β) and sex for all CHCs, respectively (i.e. allowing sexual selection to vary between the sexes). Model [1] was then compared with a reduced model with all interaction terms, $\alpha_i C_i$sex, excluded. To test whether the full model [1] was a better fit than the reduced model, we compared differences between −2 log-likelihood of the two models using a likelihood ratio test (LRT).

We tested for a cross-sex genetic correlation in the preferred CHC signal trait by scoring all males and females in the data set for the linear combination of CHCs associated with highest mating success in each sex (McGuigan *et al.*, 2011), as estimated from the Lande & Arnold (1983) ordinary least squares multiple regression described above (Table 1). In this instance, the scored trait represents the linear combination of traits under sexual selection in each sex. Genetic variances and the cross-sex genetic covariance for these traits were then estimated using restricted maximum likelihood (REML) in the multivariate mixed effects model:

$$\boldsymbol{y}_{ijk} = \boldsymbol{\mu} + \boldsymbol{d} + \boldsymbol{w} + \boldsymbol{l}_i + \boldsymbol{r}_{k_i} + \boldsymbol{\varepsilon}_{j(ik)}. \qquad (2)$$

Here, $\boldsymbol{y}_{ijk}$ is the CHC trait value of the jth individual, $\boldsymbol{\mu}$ is the population mean vector for each trait, $\boldsymbol{d}$ is the effect of experimental block, $\boldsymbol{w}$ is the effect of wing clip, $\boldsymbol{l}_i$ is the effect of the ith line, $\boldsymbol{r}_{ki}$ is the effect of the kth reference line nested within the ith line and $\boldsymbol{\varepsilon}_{j(ik)}$ is the

Table 1 Directional selection gradients for male (β_m) and female (β_f) logcontrast cuticular hydrocarbons (CHCs). Significant gradients are indicated in bold. Also shown are significance values for the sex × trait interaction from [1].

Logcontrast CHC	β_m	β_f	Sex interaction
5,9-$C_{25:2}$	−0.013	**0.120**	0.038
9-$C_{25:1}$	0.005	**−0.388**	<0.001
9-$C_{26:1}$	**−0.094**	**0.127**	<0.001
2-Me-C_{26}	−0.010	−0.006	0.951
5,9-$C_{27:2}$	**−0.769**	0.071	<0.001
2-Me-C_{28}	**−0.154**	0.051	<0.001
5,9-$C_{29:2}$	**2.535**	**−0.127**	<0.001

residual error. The error term was grouped by sex as no cross-sex covariances can be estimated at the residual level. Block and wing were modelled as fixed effects, whereas all other terms were treated as random. The genetic (co)variance matrix was estimated at the female line level due to the potential role sex-linked variance can theoretically play in the evolution of mate choice (Kirkpatrick & Hall, 2004). We used a LRT to compare whether removal of the line term significantly worsened the fit of the model. We separately estimated whether the sex-specific variances and cross-sex correlations [by specifying TYPE = UNR that estimates an unstructured covariance matrix parameterized in terms of variances and correlations rather than variances and covariances (Fry, 2004)] could be significantly distinguished from zero by constraining the values to zero using the PARMS statement in Proc Mixed (SAS version 9.3, SAS Institute) and comparing the fit of the constrained model to [2] via a LRT with 1 degree of freedom.

Finally, to estimate the cross-sex genetic correlation for male and female preference, we scored the data set for the same linear combination of CHCs but assigned the phenotypes of only the chosen individual in each trial to the genetic identity of the choosing individual. In choosers, this represents the linear combination of traits found most attractive at the population level. We then estimated the genetic variances and the cross-sex genetic covariance for these traits using [2] and again used a LRT to compare the fit of the model with and without the line term. Finally, as with the signals, we separately estimated the sex-specific variances and cross-sex correlations (using TYPE = UNR) by rerunning [2] and separately constraining the values to zero using the PARMS statement in Proc Mixed (SAS), testing the fit of each constrained model to [2] using a LRT with 1 degree of freedom. Additionally, due to the potential low power of studies estimating genetic variance in mating preferences (Chenoweth & McGuigan, 2010), we tested the potential statistical power of our approach directly, using a power analysis via simulation for a range of heritabilites (Data S1).

Results and Discussion

We ran 1967 successful mating trials from which we scored CHC phenotypes for a total of 3689 flies. We detected directional sexual selection on CHCs in both sexes (males: $F_{7,1887} = 105.19$, $P < 0.001$; females: $F_{7,1800} = 38.84$, $P < 0.001$). The variation in mating success accounted for by CHC variation (R^2_{adj} value), and total strength of selection (vector length of the selection gradients) was much greater in males than in females (males, $R^2_{adj} = 0.28$, $\|\beta_m\| = 2.66$; females, $R^2_{adj} = 0.13$, $\|\beta_f\| = 0.45$). Although the addition of non-linear selection was significant overall in both sexes, increases in R^2 were small relative to the linear component (Table 2), suggesting that the predominant form of selection on CHC's from mutual mate preferences was directional for this population. Results from our sequential model-building approach statistically confirmed differences between the sexes in directional sexual selection on these homologous signal traits (LRT: diff -2lnL = 732.2, df = 7, $P < 0.001$), in line with earlier studies in *D. serrata* (Chenoweth & Blows, 2005; Gosden *et al.*, 2012).

Table 2 Comparisons of linear and non-linear arising from male and female mate choice.

Choosing sex	Selection type	d.f.	R^2	*F* value	*P*
Male	Linear	7	0.132	39.41	<0.001
	Non-linear	28	0.026	1.94	0.002
	Full Model	35	0.158	9.43	<0.001
Female	Linear	7	0.281	109.34	<0.001
	Non-linear	28	0.038	3.65	<0.001
	Full Model	35	0.319	24.79	<0.001

Although our phenotypic comparison of sexual selection indicated differences in the suites of CHCs favoured by each sex, these attractive CHC blends could still be genetically correlated. CHCs are functionally related traits with a common biosynthetic pathway and can therefore be expected to covary (Jallon & Wicker-Thomas, 2003; Blomquist, 2010). With respect to the preferred CHC signals, our quantitative genetic analysis revealed a significant genetic basis overall (LRT removal of line term from model [2], diff -2lnL = 21.6, d.f = 3, $P < 0.001$), with nonzero variance component for both the male (diff -2lnL = 13.7, d.f = 1, $P < 0.001$) and female (diff -2lnL = 5, d.f = 1, $P = 0.025$) signal. However, the cross-sex genetic correlation between these traits was relatively small and negative (-0.312) and did not differ significantly from zero (diff -2lnL = 1, d.f = 1, $P = 0.317$; Table 3). As we found with our analysis of differences in phenotypic directional sexual selection, the lack of a significant cross-sex genetic correlation for the linear combination of traits under sexual selection suggests that males and females are targeting genetically different traits, contrary to the predictions of the correlated preference hypothesis.

Next, we tested the genetic variance in male and female preferences. We found evidence of genetic variance in mate choice overall (LRT of the line term in model [2], diff -2lnL = 43, d.f. = 3, $P < 0.001$), but this result appeared to be driven by significant genetic variance in female preferences (diff -2lnL = 43, d.f. = 1, $P < 0.001$; Table 3). In contrast, despite the presence of detectable male choice at the phenotypic level, the point estimate of the genetic variance in male preference was essentially zero

Table 3 The genetic variance/covariance matrices (**G**) for A) CHC sexual displays (*S*) and B) male and female mate preference (*P*). The cross-sex genetic covariance is below the diagonal and the genetic correlation for mutual mate choice and between male and female CHC signals is above the diagonal. Variance components or genetic correlations that differ significantly from zero ($P < 0.05$) are highlighted in bold (see Results).

	S_f	S_m
(A)		
S_f	**0.005**	−0.312
S_m	−0.003	**0.020**
	P_f	P_m
(B)		
P_f	**0.057**	<−0.001
P_m	−0.001	<0.001

(Table 3) and was nonsignificant (diff −2lnL = 0, d.f = 1, $P = 1$). Consequently, there was no evidence that the cross-sex genetic correlation for preference, which was very small (<−0.001), differed from zero (diff −2lnL = 0, d.f. = 1, $P = 1$; Table 3). Differences in phenotypic sexual selection, and the lack of any genetic correlation between the sexes in both favoured signals and preferences, are inconsistent with the correlated response hypothesis for the evolution and maintenance of mutual mate preferences in *D. serrata* and suggest that a shared genetic architecture is not responsible for male mate preferences in this species.

As with any null result, one potential explanation for the failure to detect genetic variance in male choice, and hence the absence of a cross-sex genetic correlation, is low statistical power. Low power is of particular concern here because CHCs explain less of the phenotypic variation in female mating success than in males to start with, so detection is likely to be harder as a result. Our power analysis via simulation indicated that there was adequate power to detect significant genetic variance when the broad sense heritability was as low as 5% of the total variance (Data S1). This implies that any undetected genetic variance in male preferences is likely to have been relatively small and certainly much smaller in comparison with female preference.

As our results indicate that male mate choice in *Drosophila serrata* is unlikely to be a correlated response to female choice, the question remains as to their apparent phenotypic existence and possible explanations for a lack of estimable genetic variance in this study. One possibility is that direct selection on male preferences may be sufficiently strong so as to largely exhaust standing genetic variance in them. In mating systems like *D. serrata* where males try to mate with multiple females, a male's fertilization success will be strongly tied to the fecundity of his mating partners at the time of mating (Bonduriansky, 2001). If there is a large amount of variation in female fecundity, as is generally observed for traits closely related to fitness (Houle, 1992), male mate choice is expected to evolve to target direct phenotypic indicators of this (Bonduriansky, 2001). Although female mass appears to be a common target for male mate choice in other species of *Drosophila* (Byrne & Rice, 2006), male *D. serrata* may use female CHC's as reliable indicators of female fecundity (Petfield *et al.*, 2005; Chenoweth *et al.*, 2007), potentially because their expression depends on a pool of hydrocarbons that is also involved in egg production (Wicker & Jallon, 1995). Such direct selection on male preferences may be stronger than the indirect selection on female mate preferences arising from genetic benefits to her offspring. The strength of selection on the CHC profiles for mating success in this species tends to be greater in males than in females (Rundle & Chenoweth, 2011), apparently inconsistent with the idea that genetic variation in male preference has been eliminated due to incredibly strong selection. However, we have no data on the strength of selection on the preferences themselves, making this an important topic for future work.

Female mate preferences in *D. serrata* exert strong sexual selection on male CHC traits, with male traits held at an evolutionary limit generated by contrasting natural and sexual selection (Blows *et al.*, 2004; Hine *et al.*, 2011; Delcourt *et al.*, 2012). Genetic variance in female preferences for male CHCs was previously detected in a lab-adapted population of *D. serrata* (Delcourt *et al.*, 2010), and our current results, from a panel of wild-derived lines, is consistent with this. Female choice has been shown to have a positive correlation with offspring fitness, suggestive of classic indirect (i.e. genetic) benefits to females from their choice of mates (Hine *et al.*, 2002). However, there appear to also be unidentified costs to the expression of these mate preferences in females (Rundle *et al.*, 2009), at least in the laboratory setting, and all else being equal such direct costs are expected to override any indirect benefits (Kirkpatrick & Barton, 1997). The maintenance of female preferences in this species therefore suggests that there may also be some as yet unknown direct benefits of female choice in this system.

Our findings imply that male mating preferences are unlikely to be currently maintained in this population as a genetically correlated response to selection for female preferences. Although such a result is also inconsistent with a role for the correlated response hypothesis in the origin of male preferences, it does not rule it out because current genetic (co)variances may not be indicative of those present when these preferences arose. For instance, subsequent to their origin, preference divergence driven by a higher cost and/or

direct benefit to males may have altered genetic (co) variances in response to selection. Testing hypotheses about the origin of preferences is inherently challenging but would likely involve a broader, cross-species comparative approach.

In summary, we have shown that male mate choice in *Drosophila serrata* is unlikely to be maintained as a correlated response to selection for female mate choice. Our findings of differences in the strength and direction of male and female sexual selection, no significantly detectable genetic correlation between male and female- preferred CHC blends, and no cross-sex genetic correlation for mate preferences for those CHC blends, are all contrary to the prediction of the correlated response hypothesis and suggest that male and female preferences are different traits in *D. serrata*. It is likely that the underlying selection processes responsible for their evolution differs between the sexes, with male choice potentially driven by the direct benefits of mating with highly fecund females (Chenoweth *et al*., 2007) and female mating preferences possibly arising, in part, from the indirect benefits of mating with males of high genetic quality (Hine *et al*., 2002). As our results indicate different genetic architecture underlying male and female mate preferences, any costs associated with mate choice in one sex may have limited influence on the evolution of choice in the other sex. It is unlikely that pleiotropy of mate preferences, which can theoretically cause male choice to increase in frequency (Servedio & Lande, 2006), is the basis of the observed mutual mate preferences in *D. serrata*.

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Supporting information

Additional Supporting Information may be found in the online version of this article:
Data S1 Power Analysis via Simulation.

Data deposited at Dryad: doi:10.5061/dryad.t0g84

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