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SEX-SPECIFIC EVOLUTIONARY POTENTIAL OF PRE- AND POSTCOPULATORY REPRODUCTIVE INTERACTIONS IN THE FIELD CRICKET, *TELEOGRYLLUS COMMODUS*

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Mate choice often depends on the properties of both sexes, such as the preference and responsiveness of the female and the sexual display traits of the male. Quantitative genetic studies, however, traditionally explore the outcome of an interaction between males and females based solely on the genotype of one sex, treating the other sex as a source of environmental variance. Here, we use a half-sib breeding design in the field cricket, *Teleogryllus commodus*, to estimate the additive genetic contribution of both partners to three steps of the mate choice process: the time taken to mate; the duration of spermatophore attachment; and the intensity of mate guarding. Rather than each sex contributing equally to the interactions, we found that genetic variation for latency to mate and spermatophore attachment was sex-specific, and in the case of mate-guarding intensity, largely absent. For a given interaction, genetic variation in one sex also appears to be largely independent of the other, and is also uncorrelated with the other traits. We discuss how pre- and postcopulatory interactions have the potential to evolve as an interacting phenotype, but that any coevolution between these traits, due to sexual selection or sexual conflict, may be limited.

KEY WORDS: Genetic correlations, heritability, interacting phenotypes, sexual conflict, sexual selection..

Reproductive interactions between males and females are central to the theory of mating system evolution by both sexual selection and sexual conflict. Competition between males for access to mates and the subsequent expression of choice by females can favor the elaboration of a suite of male sexual traits (Andersson 1994). Similarly, differences in the evolutionary interests of males and females can select for antagonistic traits that allow one sex to manipulate the outcome of the reproductive interaction in their favor (Parker 1979). By combining the selection generated by mate choice or sexual conflict with the underlying genetic architecture of the target traits, empirical studies have shown how reproductive interactions can influence the evolution of male sexual traits and sexual dimorphism (Blows 2007) or the coevolution of male manipulative traits and female resistance (Arnqvist and Rowe 2005). Understanding the evolution of the reproductive interactions themselves is more problematic, as traits that are shaped by interactions, termed interacting phenotypes (Moore et al. 1997), are difficult to define as the property of one individual, or in the case of mate choice, one sex.

Common metrics of mate choice, such as latency to mate or mating rate, are often treated as estimates of either male attractiveness or of female choosiness, when in fact the observed phenotype

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is a composite of both behaviors. A male's mating success, for example, will depend on both the degree to which he expresses the sexual traits that females prefer and on the willingness of the female he is courting to mate (Jennions and Petrie 1997; Procter et al. 2012). Similarly, interlocus sexual conflict over the expression of a "conflict trait" (Lessells 2006), such as copulation duration or mating frequency, rests on the ability of males to coerce or manipulate females, and of females to resist those manipulations (Arnqvist and Rowe 2005). Viewing the mating behavior of each sex in insolation, therefore, may capture only a fraction of the total genetic variability in the resulting trait, potentially ignoring genetic contributions of the mating partner, as well as possible interactions between both partners' genotypes (Moore et al. 1997; Wolf et al. 1998).

The development of analytical approaches to studying such complex interactions (Moore et al. 1997; Wolf et al. 1999; McGlothlin and Brodie III 2009) has led to a growing number of studies estimating the genetic contribution of both a focal individual and their social partners, as well as highlighting how social interactions can modify selection responses (Brommer and Rattiste 2008; Teplitsky et al. 2010; Wilson et al. 2011). A study of female reproductive performance in the red-billed gull, for example, revealed that female laying date depends on the genotypes of males and females, but the male and female genetic contributions are negatively correlated (Brommer and Rattiste 2008). Within the broader interacting phenotype literature, however, empirical evidence is generally limited to classic model species (Wolf 2003; Petfield et al. 2005; Mutic and Wolf 2007; Bacigalupe et al. 2008) or species where extensive pedigrees are known due to animal breeding (Muir 2005; Bijma et al. 2007; Bergsma et al. 2008). For other species where the genetic basis of mate choice is less well described, the first steps are to simultaneously characterize how the genotypes of both males and females contribute to the interactions that define male attractiveness and female choice, or are the target of interlocus sexual conflict.

In this study, we investigated the extent to which additive genetic variation in both males and females contributes to pre- and postcopulatory mating interactions in the black field cricket, *Teleogryllus commodus*. In this species, females prefer males based on specific properties of the male advertisement and courtship call, together with body size (Brooks et al. 2005; Hall et al. 2008). Moreover, the same males who attract the most females in the field via increased calling effort (Bentsen et al. 2006) will also be favored by precopulatory choice via the shortest latency to mate (Shackleton et al. 2005), as well as postcopulatory choice through increased attachment time of their spermatophore and hence elevated sperm transfer (Bussière et al. 2006; Hall et al. 2010a). Furthermore, sexual conflict manifests over the removal of the spermatophore after copulation. Males aggressively oppose spermatophore removal by the female immediately following copulation (Loher and Rence 1978), with unattractive males harassing females the most vigorously (Bussière et al. 2006).

Although previous studies in *T. commodus* have characterized additive genetic variation in the traits underlying the male advertisement call (Hunt et al. 2007; Lailvaux et al. 2010) and courtship call (Hall et al. 2010b), quantitative genetic estimates of pre and postcopulatory mate choice are lacking. Here, we used a half-sib breeding design in which males and females of known pedigree were randomly mated and then the subsequent mating interactions characterized in terms of: the time taken to mate; the duration of spermatophore attachment; and the intensity of mate guarding. To analyze these data, we first approach each measurement of mate choice as an interacting phenotype and simultaneously estimate the sex-specific genetic variation in each trait. We ask whether the genetic variation is shared equally between the sexes for a common trait, and if the genetic variation in one sex is independent of the other. We then follow a more classical quantitative genetic approach and treat male and female mating behaviors as separate traits. By estimating the within- and between-sex genetic correlations in the different mating interactions, we evaluate the potential for coevolution between pre- and postcopulatory male attractiveness and female choice in this species.

Methods

The animals used in this experiment were the fourth-generation offspring of a large, well-mixed laboratory culture of *T. commodus*, collected from Smiths Lake (32°22′S, 152°30′E), New South Wales, Australia. Using a half-sib breeding design, we mated 54 sires each to six different dams, resulting in 237 full-sib families as nine males died before completing the matings and 43 dams failed to produce any offspring. From each of the full-sib families we collected 25 offspring at random, and raised them individually in plastic containers (7 × 7 × 5 cm) provided with cat food (Friskies Go-Cat Senior, Nestlé Australia, Sydney), water, and shelter. We kept the crickets in a constant temperature room (28°C, 14:10 h light:dark regime) and replaced food and water weekly. The positions of the containers within the constant temperature room were changed weekly to minimize any localized environmental effects. The offspring collected from each family were used in the behavioral trials outlined below.

BEHAVIORAL MEASURES

In a series of behavioral trials, we measured the mating interactions of males and females from the half-sib breeding design. Using the offspring from each full-sib family, we separately paired four males and four females with an unrelated individual, randomly chosen from another family. We conducted the trials over two nights every three days, using crickets that were between

10 and 12 days posteclosion. Each mating pair was placed in an arena consisting of a medium-sized plastic container (17 × 12 × 8 cm) lined with damp paper towel and observed in a room dimly lit by red incandescent lights (40 W, Philips Lighting, The Netherlands) to minimize any observer disturbance.

On the first night, we mated all available females to a random male from the same breeding design and prevented the removal of the spermatophore for at least 45 min by allowing males to guard the female. We recorded whether the male was in antennal contact with the female every 6 min for up to an hour, allowing mate-guarding intensity to be estimated as the percentage of observations in which guarding was observed. It has also been previously shown that the attractiveness of the first random male has no influence on the reproductive opportunities of the second focal male (Bussière et al. 2006). On the second night, we then randomly generated new mating pairs and recorded the latency to mate as the time taken from the start of the trial until the female mounts the male. We then removed the male immediately following copulation, allowing each female to control spermatophore removal freely. We recorded the time of spermatophore attachment until it was removed. If a mating pair failed to mate successfully they were re-mated on the subsequent evening. In total, we were able to measure mate guarding for 984 mating pairs, and latency to mate plus spermatophore attachment for 925 mating pairs.

STATISTICAL ANALYSIS

We used two complementary approaches to estimate the additive genetic contribution of each male and female partner to a given trait, using restricted maximum likelihood as implemented using ASReml-R (version 3.0.1, Butler et al. 2009) and R (version 2.14.1, http://www.R-project.org). First, the contribution of both male and female partners to a single reproductive interaction (y) resulting from a mating pair (i) is modeled as:

$$y_i = \mu + sire_f + dam_f + sire_m + dam_m + e_i,$$

where μ is the population mean, $sire_f + dam_f$ and $sire_m + dam_m$ are the sire and dam (nested within sire) family background of females and males, respectively, and e_i is the residual term. Based on this model, we could estimate the sex-specific sire and dam heritabilities, as well as the combined genotypic heritability (i.e., the mean of the sire and dam estimates, Becker 1992). At the level of the sire, we could also test for a genetic association between male and female effects by estimating the genetic correlation (herein $r_{sire.mf}$) between $sire_f$ and $sire_m$, as per a crossed random effect (see Butler et al. 2009).

Significance tests for random effects were conducted using a likelihood-ratio test based on −2 × the difference in log likelihood between the full model and a model where the random effects of interest were constrained to be zero. For heritabilities, we report only one-tailed P-values based on the tested hypothesis that $h^2 > 0$. We also assessed whether there were differences between the sexes in their genetic contribution to each trait, by forcing variances to be equal between $sire_f$ and $sire_m$, and dam_f and dam_m, and then comparing this model to the full, unconstrained model.

Finally, to supplement the interacting phenotype approach to the analyses of each individual reproductive interaction, we considered latency to mate, spermatophore attachment and mate-guarding intensity for each sex as different traits, and estimated the within- and between-sex genetic relationships using a series of bivariate nested half-sib models. Additive genetic variances and covariances were estimated based on the sire component, using the following model:

$$\mathbf{y} = \mathbf{X}ß + \mathbf{Z_1 s} + \mathbf{Z_2 d} + \mathbf{e},$$

where $\mathbf{y}$ is a vector of observations corresponding to the bivariate combinations of sex-specific mate choice traits, $\boldsymbol{\beta}$ is a vector of mean phenotypes, $\mathbf{s}$ is the vector of random additive effects of sire, $\mathbf{d}$ is the vector of random dam effects, and $\mathbf{e}$ is a vector of residual effects. $\mathbf{X}$, $\mathbf{Z_1}$, and $\mathbf{Z_2}$ are design matrices relating observations to the fixed, sire, and dam effects, respectively. Given the lack of dam variance for male spermatophore attachment and male mate-guarding intensity, we constrained all dam covariances involving these traits to zero. We assumed the between-sex residual variances to be independent and only estimated within-male and within-female residual covariances; although not in the case of mate-guarding intensity as these estimates were made in separate mating trails. Significance tests for variances, covariances, and correlations were conducted as above using log likelihood-ratio tests.

Results

INTERACTING PHENOTYPES AND PRE- AND POSTCOPULATORY MATE CHOICE

For each measure of pre- and postcopulatory interactions (latency to mate, spermatophore attachment time, and mate-guarding intensity), we estimated the additive genetic contribution of each male and female partner to a given trait within a single model. The resulting sex-specific sire, dam, and genotypic heritability estimates are shown in Table 1. Maternal effects appear to be negligible, as the sex-specific sire and dam components were largely concordant and not significantly different from each other (all $P > 0.4$, tests not shown). For latency to mate and spermatophore attachment, there appears to be some asymmetry in how males and females share the genetic variance in a reproductive interaction. Focusing on the genotypic heritability estimates, only two overall heritabilities were significant with 23% of the variation in latency to mate explained by the male-specific additive genetic

Table 1. The genetic contributions of males and females to pre- and postcopulatory mating interactions. Sire, dam, and genotypic heritabilities were estimated using the variances components from a single model incorporating the sire–dam information of both individuals' parents. Latency to mate refers to the time taken to mate from the start of a behavioral trial (log[s], mean = 6.250, SD = 1.296), spermatophore attachment to the time taken for a female to remove the male spermatophore following mating ($\sqrt[3]{s}$, mean = 12.120, SD = 4.059), and mate-guarding intensity to the proportion of observations where male guarding behaviors were observed ([arcsine transform] × 10, mean = 8.976, SD = 2.831). Significant ($P < 0.05$) and marginally significant ($P < 0.1$) values are highlighted in bold.

	Latency to mate			Spermatophore attachment			Mate-guarding intensity		
	h^2	SE	*P*-value	h^2	SE	*P*-value	h^2	SE	*P*-value
Female-specific estimates									
Sire	0.025	0.053	0.311	**0.326**	**0.112**	**<0.001**	0	–	0.999
Dam	0.049	0.113	0.332	**0.180**	**0.120**	**0.055**	0	–	0.999
Genotypic	0.037	0.053	0.349	**0.253**	**0.071**	**<0.001**	0	–	0.999
Male-specific estimates									
Sire	**0.211**	**0.100**	**0.005**	0.006	0.041	0.434	0.048	0.051	0.141
Dam	**0.255**	**0.128**	**0.015**	0	–	0.999	0	–	0.999
Genotypic	**0.234**	**0.067**	**<0.001**	0.003	0.021	0.493	0.023	0.025	0.280

component and 25% of the variation in spermatophore attachment time explained by the female-specific additive component. In contrast, for mate-guarding intensity, both male- and female-specific heritabilities were either low and nonsignificant or too small to estimate.

Sire, dam, and genotypic heritabilities, therefore, appear to be higher for male-specific estimates of latency to mate, whereas the reverse is true for spermatophore attachment. Constraining sire and dam variances to be equal between the sexes revealed that genetic estimates of spermatophore attachment are strongly sex-biased ($\chi^2_2 = 13.02$, $P[h^2_{\mathrm{M}} < h^2_{\mathrm{F}}] = 0.001$, $P[h^2_{\mathrm{M}} \neq h^2_{\mathrm{F}}] = 0.002$), whereas the differences between male and female estimates of latency to mate are at least partially supported ($\chi^2_2 = 5.06$, $P[h^2_{\mathrm{M}} > h^2_{\mathrm{F}}] = 0.040$, $P[h^2_{\mathrm{M}} \neq h^2_{\mathrm{F}}] = 0.080$). The genetic variance in one sex also appears to be largely independent of the other, as the genetic correlations between male and female sire components within a given model were not significant for both latency to mate ($r_{sire.mf} \pm \mathrm{SE} = 0.155 \pm 0.659$, $\chi^2_1 = 0.058$, $P = 0.809$) and spermatophore attachment ($r_{sire.mf} \pm \mathrm{SE} = 0.525 \pm 1.929$, $\chi^2_1 = 0.244$, $P = 0.621$).

WITHIN- AND BETWEEN-SEX GENETIC CORRELATIONS

To complement our decomposition of individual reproductive traits into male and female genetic components, we also explored the within- and between-sex genetic relationships between estimates of pre- and postcopulatory mate choice. The genetic variances, covariances, and correlations between sex-specific estimates of latency to mate, spermatophore attachment, and mate-guarding intensity are shown in Table 2. In these analyses, we did not include mate-guarding intensity as a female trait due to the lack of genetic variation in this context (see Table 1). Overall, there was little evidence that any traits were genetically correlated both within a single sex, and between the two sexes. Given the generally low levels of genetic variation (Table 1 heritabilities and Table 2 bold values), the lack of significant genetic covariances and correlations is not surprising, with the magnitude and direction of the estimates uninformative as correlations and covariances are undefined when one trait has heritability equal to zero (Lynch and Walsh 1998). However, the additive genetic variation of both female spermatophore attachment times and male latency to mate was significant, and yet the correlation between these two traits was still very small and not significantly different from zero.

Discussion

In many species, mate choice depends on a number of properties of both sexes such as the preference and responsiveness of the female, the sexual display traits underlying male attractiveness and the coercive ability of the male. Any interaction between males and females, therefore, has the potential to be influenced by a suite of genes acting independently in each sex and, potentially, in combination. Indeed, with the growing evolutionary theory of interacting phenotypes (Moore et al. 1997; Moore and Pizzari 2005; McGlothlin and Brodie III 2009), the outcome of male–female reproductive interactions is expected to depend on the genetic variation in males, the genetic variation in females, and how they interact. In this study, we estimated the additive genetic contribution of male and female partners to three sequential steps of the mate choice process: the time taken to mate after first contact occurs between a male and female; the duration of spermatophore

Table 2. The genetic relationships between sex-specific estimates of latency to mate, spermatophore attachment, and mate-guarding intensity (SE in brackets). Genetic correlations in italic are above the diagonal, and genetic covariances of traits are below the diagonal (estimated using separate bivariate models). Additive genetic variances of traits are in bold along the diagonal (estimated from separate univariate models). The gray shading indicates the subset of the genetic relationships featuring between-sex genetic correlations and covariances (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).

	Female traits			Male traits		
	Latency	Attachment	Guarding	Latency	Attachment	Guarding
Female-specific estimates						
Latency to mate	**0.136**	*0.192*	0	*0.313*	*0.126*	0
	(0.112)	*(0.382)*	–	*(0.436)*	*(0.718)*	–
Spermatophore attachment	0.166	**5.408*****	0	*0.007*	*0.141*	*– 0.516*
	(0.332)	**(1.960)**	–	*(0.287)*	*(0.496)*	*(0.461)*
Mate-guarding intensity	0	0	0	0	0	0
	–	–	–	–	–	–
Male-specific estimates						
Latency to mate	0.070	0.009	0	**0.375****	*– 0.032*	*– 0.681*
	(0.098)	(0.408)	–	**(0.174)**	*(0.552)*	*(0.460)*
Spermatophore attachment	0.036	0.252	0	– 0.015	**0.608**	– 0.079
	(0.205)	(0.877)	–	(0.265)	**(0.797)**	(0.850)
Mate-guarding intensity	0	– 0.721	0	– 0.277	– 0.038	**0.381**
	–	(0.624)	–	(0.193)	(0.406)	**(0.404)**

attachment (and, thus, the amount of sperm transferred); and the intensity of mate guarding and the ability of males to coerce and females to resist postcopulatory outcomes.

Rather than males and females contributing equally to genetic variation in reproductive interactions, we found that genetic variation for latency to mate and spermatophore attachment appears to be limited to one sex, or in the case of mate-guarding intensity, largely absent (Table 1). Such results are surprising, as males and females both participate at each of these three key stages, and it seems reasonable to expect that each sex introduces significant variation at each stage. However, even though the active cooperation of a female is required for successful mating in *T. commodus* (Loher and Rence 1978), genetic variation in latency to mate was limited largely to the male. In contrast, the duration of spermatophore attachment, a trait that is phenotypically correlated with male attractiveness (Bussière et al. 2006) and courtship call properties (Hall et al. 2008), was significantly heritable only when considered as a trait of the female. Mate-guarding intensity showed negligible genetic variance, suggesting little segregating genetic variation in either the ability of males to coerce or in the ability of females to resist this postcopulatory behavior.

Our results highlight how some, but not all, of interacting phenotype theory applies to mate choice in *T. commodus*. Each sex, for example, did not always contribute substantially to the genetic variability of a shared trait, and the genetic contribution of one sex does not appear to be strongly associated with the genetic contribution of the other (i.e., nonsignificant $r_{sire.mf}$ estimates). Rather, the key insight is that the phenotype of one sex may still evolve due to the significant additive genetic variation contributed to the trait by their partner (Moore et al. 1997). This results in some counterintuitive predictions. For example, we predict that spermatophore attachment time (a measure thought to capture male postcopulatory attractiveness, Bussière et al. 2006; Hall et al. 2010a) is less likely to evolve in response to the success it confers on males in sperm competition and more likely to change due to selection on the speed with which females remove the spermatophore. Conversely for female choice, how quickly a female chooses to mate has little capacity to evolve when selection favors faster or slower choices, but sexual selection on male attractiveness has the potential to change the time it takes females to respond.

The lack of significant genetic correlations between male and female behaviors, however, suggests that direct coevolution between these traits may be limited. Theory predicts that female mate choice will potentially evolve either as a result of direct selection to minimize the direct costs of mating or as an indirect response to another genetically correlated trait under selection, such as male attractiveness (Kirkpatrick 1996; Iwasa and Pomiankowski 1999; Kokko et al. 2002). Indeed, based on precopulatory mating decisions, our results suggest that choosy females can potentially benefit from the indirect, genetic benefits acquired for their offspring in subsequent generations (Fisher 1930), as attractive males, based on latency to mate, will also sire attractive sons. A component of female choice, spermatophore removal, was also heritable. Yet all estimated genetic covariances and correlations between sex-specific estimates of latency to mate and spermatophore attachment were nonsignificant (Table 2). Genetic variances and covariances related to male and female antagonistic interactions over mate guarding were also negligible (Tables 1 and 2). Thus, as each sex contributes genetically to at least one reproductive interaction, components of male attractiveness and female choice have the potential to evolve, but any coevolution directly between these traits, whether due to sexual selection or sexual conflict, appears to be limited.

In summary, resolving the contributions of both sexes to genetic variance in reproductive interactions, and estimating the covariances between male and female contributions, holds great potential for testing models of sexual selection and mate choice evolution. In this study, it helped to reveal how genetic variation in a single trait is not shared equally and that the potential for any genetic interaction between males and female may be limited. Although our results offer new insight into the sex-specific evolutionary potential of mate choice evolution, it is important to acknowledge the limitations of the half-sib breeding design for characterizing associations between male and female genetic contributions. Estimations of crossed random effects (i.e., $r_{sire.mf}$ estimates) are sensitive to sample size, and while our design was larger than most, our power to estimate such effects is limited by the random pairing of individuals from only 54 sires. It is also likely that the balance of genetic variation between males and females may change in different mate choice scenarios. For example, the female contribution to latency to mate could increase when females are virgins, or the male influence on attachment times may be higher if they are allowed to prevent spermatophore removal. Nonetheless, our approach and findings highlight the presence of complex, but ultimately tractable nuances to the genetic basis of pre- and postcopulatory mate choice.

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