

No Apparent Indirect Genetic Benefits to Female Red Flour Beetles Preferring Males with Intense Copulatory Courtship

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Received 20 Apr. 2005—Final 27 Dec. 2005

Whether females gain indirect genetic benefits through mate choice is a controversial issue since this requires additive genetic variance in the preferred male traits. Condition dependence could maintain the necessary genetic variance by linking the expression of male traits to the supposedly large number of genes affecting condition. Copulating males of the red flour beetle *Tribolium castaneum* rub their legs along the female elytra. Females favor males with vigorous rubbing through cryptic female choice. We measured the repeatability and heritability of this behavior and assessed its potential use as indicator of viability and condition. We found genetic variance in larval to adult survival and in the rate of leg rubbing in males. However, the rate of leg rubbing was not related to offspring survival or condition dependent. The genetic variance in leg rubbing was mostly non-additive with very low narrow sense heritability. Therefore, we failed to document any indirect genetic benefits to choosy females through viability of their offspring or attractiveness of their sons.

KEY WORDS: Condition dependence; copulatory courtship; cryptic female choice; heritability; indirect genetic benefits; *Tribolium castaneum*.

INTRODUCTION

Although there is now much empirical support for the importance of female mate choice, whether variance in the genetic quality of males is a major driving force in the evolution of female mate preferences is still a matter of controversy and debate (Andersson, 1994; Kirkpatrick and Ryan, 1991; Møller and Alatalo, 1999; Shuster and Wade, 2003). Females would gain fitness benefits by preferring males with certain traits if offspring of these males had higher than average attractiveness or viability and this resulted in a high fitness (Andersson, 1994; Houle and Kondrashov, 2002). This requires some heritability of fitness caused by additive genetic variation in male attractiveness or viability. If females keep choosing to

mate with the most attractive males, then additive genetic variance in male attractiveness should be depleted and females would no longer gain indirect genetic benefits from being choosy. That females nonetheless often appear to be choosy has been termed the “lek paradox” (Borgia, 1979; Kirkpatrick and Ryan, 1991) because this paradox is especially evident in lekking species where females derive no material benefits from males and a few males obtain a high proportion of the matings. A resolution of the paradox requires a mechanism maintaining sufficient additive genetic variance in male fitness. Rowe and Houle (1996) suggested that if the expression of sexually selected traits were condition dependent then these traits could capture the genetic variance for individual condition. Defined as the amount of resources available for allocation to fitness enhancing traits (Lorch *et al.*, 2003; Tomkins *et al.* 2004), condition is likely to be influenced by a large number of genes and genetic variance in condition may therefore be substantial even in the face of selection. This may provide the postulated indirect genetic benefits to choosy females (Rowe and Houle, 1996).

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Few studies have attempted to evaluate the genetic basis of condition (Tomkins *et al.*, 2004). However, several studies have found correlations between male traits preferred by females and viability manifested as offspring survival (see Møller and Alatalo, 1999 for a review of good genes effects). With only one exception, the male traits studied were involved in pre-copulatory (“overt”) female choice. It is now becoming increasingly clear that post-copulatory (“cryptic”) female choice has driven the evolution of male courtship behavior taking place during copulation (Eberhard, 1996; Edvardsson and Arnqvist, 2000; Tallamy *et al.*, 2002; Thornhill, 1983). Therefore, understanding the evolution of female preferences used in cryptic choice is an essential part of the study of sexual interactions between males and females. Yet, only one study so far has tried to link male copulatory courtship behavior with indirect benefits to females and test whether these behaviors can serve as honest indicators of male genetic quality (Tallamy *et al.*, 2003). Tallamy *et al.* (2003) found that females of the spotted cucumber beetle, *Diabrotica undecimpunctata howardi*, may gain indirect genetic benefits by only accepting spermatophores from males with a vigorous copulatory courtship behavior. Males of this species use their antennae to stroke females when mounted and fast stroking males sire fast stroking sons, which are also more successful as mates (Tallamy *et al.*, 2002, 2003). However, Tallamy *et al.* (2003) did not find any effects of male stroking speed on offspring viability.

The red flour beetle, *Tribolium castaneum*, is a cosmopolitan pest on stored grain (Sokoloff, 1972). Males of this species perform a copulatory courtship behavior. They stand on the backs of their mates during copulation and rub their legs, in bouts of one to a few strokes, along the lateral edges of the female elytra. Males with a high rate of leg rubbing have been shown to be favored through cryptic (post-copulatory) female choice with female perception of male leg rubbing being important for relative male paternity success when females have mated with two males (Edvardsson and Arnqvist, 2000; Bloch-Qazi, 2003). A similar male behavior, involving bouts of tapping with head and forelegs, acts as pre-copulatory courtship in the dung beetle *Onthophagus taurus* and has been shown to be condition dependent (Kotiaho *et al.*, 2001). In the present study we measure the repeatability and heritability of the leg rubbing behavior in *T. castaneum* and test whether or not it could be used by females as an indicator of viability and condition.

METHODS

The beetles used in this study originated from *Tribolium castaneum* stocks provided originally by the *Tribolium* stock centre at the US grain marketing research laboratory in Manhattan, Kansas in 1998. Two strains were used, the wildtype Georgia strain (GA-1) and the black strain. The former strain was collected in a farmer’s corn bin in Georgia (USA) in 1980, and is genetically heterogeneous (Beeman RW, personal communication). The latter strain carries a semidominant autosomal mutation making the adults black instead of their wildtype chestnut color (Sokoloff *et al.*, 1960). All beetles were maintained at 30°C and 70% relative humidity in dark incubators. A mixture of 19 parts whole-wheat flour and one part dry brewer’s yeast was used as culture medium (Sokoloff, 1972). All individuals used in the experiment were sexed as pupae and between 11 and 20 days post-eclosion at the time of their first mating. Mating experiments and behavioral observations were carried out at room temperature (20–22°C) and under diffuse room lighting.

Matings were staged in petri dishes (10 mm high, 35 mm diameter) where the bottom was covered with a thin layer of flour-yeast medium. In case virgin males behave differently during copulation compared to experienced males, each male was given the opportunity to mate with a virgin female not included in the experiment, 24 hours before the first experimental mating. Males that failed to mate within 1 hour were not included in the experiment. The males that did mate ($N=31$) were given the opportunity to mate (1 hour each time) with three more virgin wildtype females with 24 hours between each mating. Most males ($N=29$) mated three times. During each mating, we used the EthoLog 2.2.5 software (Otoni, 2000) to record time until mating, copulation duration and every bout of strokes of each leg performed by the males. Following the matings, each female was allowed to oviposit in 15 g of sifted flour-yeast medium for 5 days.

The medium was sieved 10 days after the last day of oviposition and we selected 20 larvae randomly from each petri dish and divided them into two groups of 10 larvae. One group was placed in a petri dish containing 20 g of fresh flour-yeast medium (low-density treatment) and the other in a petri dish containing 10 g of flour-yeast medium together with 30 larvae of the black strain which were put in at the same time and 10 adult males of the Georgia strain which had been placed in the medium 4 days earlier

(high-density treatment). Thus, every male could sire the offspring of three females and each female had offspring that were reared in the low-density treatment and other offspring that were reared in the high-density treatment. Larvae in the low-density treatment should suffer virtually no competition whereas larvae in the high-density treatment should experience conditions similar to the conditions in the stock cultures. *T. castaneum* larvae are sometimes cannibalistic mainly consuming eggs (Sokoloff, 1974). Individuals reared under high-density may therefore benefit from improved feeding opportunities. However, this was unlikely to occur in the present study since no eggs were available and all larvae were of a similar age.

We checked the petri dishes regularly and collected all pupae from them as they formed. When the adult beetles emerged they were scored for body color and sexed and the number of surviving wildtype beetles was recorded. Depending on the number of surviving sons, up to five sons from each female were given the opportunity to mate with virgin females in the same way as described above. Those that mated within an hour were mated to another virgin female 24 hours later. During the second and focal mating, we quantified the leg rubbing behavior and recorded time until mating and copulation duration.

We used the data from the parental and offspring matings to assess the heritability, repeatability and condition dependence of the copulatory courtship behavior. The value of the copulatory courtship behavior as indicator of offspring viability was analyzed using the data on male leg rubbing and offspring survival. Data were transformed, when necessary, to meet the assumptions of the statistical models used.

RESULTS

Repeatabilities

The repeatabilities (r) of time until mating, copulation duration and the leg rubbing behavior measured over three matings involving the same males but different females were calculated as the intraclass correlation coefficients using variance components from analyses of variance presented in Table I (Lessells and Boag, 1987).

Rate of leg rubbing showed significant repeatability ($r=0.333$). Time until mating ($r=0.105$) and copulation duration ($r=0.035$) on the other hand, did not. There were no significant changes in the average rate of

leg rubbing, time until mating or copulation duration over the three consecutive matings. Given the sample sizes used in our analyses, the statistical power was 60% for detecting a repeatability of 0.24 and 80% for detecting a repeatability of 0.32.

Offspring Survival

We analyzed the genetic effects of sires and the effects of the density treatments on offspring survival in an ANOVA (Table II). To attain a balanced data set only sires with two or three successful matings were included and only the first two matings were used in sires with three successful matings. Sire was important for offspring survival with the arcsine-transformed proportion of offspring surviving showing significant repeatability over the two females ($r=0.303$). The density treatment also had a significant effect on survival with a higher proportion of offspring surviving in the low-density treatment (mean = 0.87) than in the high-density treatment (mean = 0.77). Sire and treatment did not interact in their effects on survival.

To test whether the rate of leg rubbing of sires was associated with survival of their offspring, we performed an ANCOVA of offspring survival using larval environment as a factor and the mean rate of leg rubbing of sires as a continuous covariate. The mean offspring survival of each sire including the same matings as above was used. There was no significant effect of the rate of leg rubbing on the proportion of surviving offspring ($F_{1,18}=0.086$,

Table I. One-way Analyses of Variance of Time until Mating, Copulation Duration and the Rate of Leg Rubbing, based on Measures from Three Consecutive Matings for Individual Males

Source	df	Time until mating		Copulation duration		Rate of leg rubbing	
		<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Male	26	1.34	0.179	1.11	0.362	2.15	0.009
Error	53						

Table II. Analysis of Variance of Proportion of Surviving Offspring in the Two Larval Density Treatments

Source	df	MS	<i>F</i>	<i>p</i>
Sire	10	0.110	2.75	0.024
Treatment	1	0.235	5.87	0.025
Sire*Treatment	10	0.019	0.49	0.881
Error	21	0.040		

$p=0.77$) and there was no interaction between rate of leg rubbing and larval environment ($F_{1,18}=0.941$, $p=0.71$). The Pearson correlation between rate of male leg rubbing and arcsine-transformed proportion of surviving offspring was not significant in either larval environment (low density: $r=0.199$, $p=0.35$, $N=24$; high density: $r=-0.288$, $p=0.17$, $N=24$).

Heritability

A total of 24 males and 38 females produced sons surviving to adulthood. Because each dam produced an uneven number of offspring, and an unequal number of dams per sire produced any surviving offspring, the half-sib data for estimation of quantitative genetic parameters were highly unbalanced. We first used restricted maximum likelihood (REML) to estimate the full nested mixed models (SAS® PROC MIXED). In contrast to other methods, REML offers methods for testing for random effects under a range of circumstances even when the data are unbalanced (which is typically the case with biological data on sets of relatives), as well as for fixed effects (e.g., Falconer and Mackay, 1996; Shaw, 1987; Shaw *et al.*, 1995). However, due to negative variance components (see Shaw 1987 for a discussion of the non-negativity constraint and REML estimation) statistical inference based on the half-sib data was deemed unreliable, and the data were highly unbalanced with many missing cells. To reduce the degree of unbalance in our data, we restricted our data set to include only one dam per sire (the dam with most surviving sons was retained in the data set) and then conducted mixed model analyses of variance of these full sibs, again using REML estimation.

The analyses of full sib data showed marginal effects of sire on both the time until mating (Table III) and the rate of leg rubbing of their sons (Table IV). Moreover, density treatment interacted with sire in its effect on both these dependent variables if only marginally on time until mating (Fig. 1). We note that it is difficult to envision any common environmental effects, such as maternal effects, that might have contributed to these results. These analyses therefore suggest both genetic variance in these behaviors and an effect of the conditions under which the beetles have been reared on their phenotypic expression. However, there were no significant main effects of treatment (Tables III and IV). This suggests that although the rearing environment affects different genotypes differently, the measured traits are not generally condition dependent in their expression. On

average, beetles reared in the high-density treatment did not have a lower rate of leg rubbing or take longer time to initiate matings, contrary to what would be expected if these traits were condition dependent.

REML estimators of variance components are known to be negatively biased when G matrices are non-positive and non-definite (see Shaw, 1987). Because of this, and because of the limited information content offered by full sib data (Falconer and Mackay, 1996), we base our estimates of additive genetic effects on parent-offspring analyses. In general, estimates of genetic parameters based on parent-offspring resemblance are more accurate and reliable than those derived from full-sib analyses (Falconer, 1973; Falconer and Mackay, 1996). We used conventional parent-offspring regressions, based on values of sires and the mean values of their sons, to estimate narrow-sense heritabilities for the traits included in our analyses. Narrow sense heritability was derived directly from these regressions, as $h^2=2\beta$ (Falconer and Mackay, 1996). To control for any interactions between the measured traits and treatment we first performed ANCOVAs with the paternal trait value as the independent variable and with density treatment as a categorical covariate. A significant interaction term would call for the calculation of separate heritabilities for the two environments.

Time until Mating

There were no significant effects of time until mating in sires ($F_{1,42}=0.015$, $p=0.90$) and treatment

Table III. The Results of a Mixed Model Analysis of Variance of Time until Mating, Based on Full Sib Data and Using Restricted Maximum Likelihood (REML) Estimation

Effect	df	F	p
Sire	23	1.54	0.073
Treatment	1	1.23	0.270
Sire*Treatment	23	1.54	0.073
Residual	112		

Table IV. The Results of a Mixed Model Analysis of Variance of the Rate of Leg Rubbing, Based on Full Sib Data and Using Restricted Maximum Likelihood (REML) Estimation

Effect	df	F	p
Sire	23	1.58	0.060
Treatment	1	0.12	0.730
Sire*Treatment	23	1.65	0.044
Residual	112		

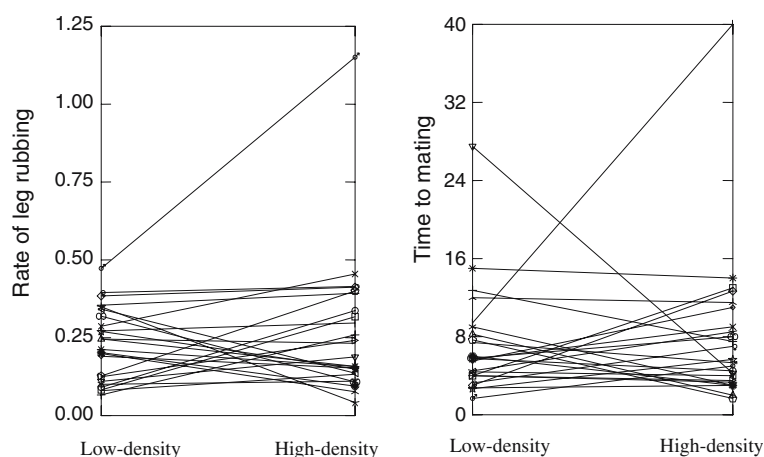


Fig. 1. Average rate of leg rubbing (bouts of rubbing per second) and time until mating (minutes) of males reared in the low-density treatment (1) and their full-sib brothers reared in the high-density treatment (2).

($F_{1,42} = 0.058$, $p = 0.81$) on time until mating in the offspring. The interaction between the two was not significant ($F_{1,42} = 0.153$, $p = 0.70$). The parent–offspring regression, for the two treatments combined revealed no significant heritability ($\beta = -0.030$, $SE = 0.108$, $N = 24$, $p = 0.78$, see Table V for heritability estimate).

Copulation Duration

Sire copulation duration had no significant effect on offspring copulation duration ($F_{1,43} = 0.064$, $p = 0.80$) and nor did treatment ($F_{1,43} = 0.223$, $p = 0.64$). There was no significant interaction ($F_{1,43} = 0.215$, $p = 0.65$) and the heritability of copulation duration was not significant ($\beta = -0.154$, $SE = 0.184$, $N = 24$, $p = 0.41$, see Table V for heritability estimate). Again, the two treatments were analyzed in the same parent–offspring regression.

Rate of Leg Rubbing

Neither sire rate of leg rubbing ($F_{1,43} = 0.072$, $p = 0.79$) nor treatment ($F_{1,43} = 1.925$, $p = 0.17$) had

significant effects on offspring rate of leg rubbing. The interaction term was not significant ($F_{1,43} = 3.017$, $p = 0.09$) and the parent–offspring regression for the two treatments combined showed no significant heritability of rate of leg rubbing ($\beta = -0.032$, $SE = 0.173$, $N = 24$, $p = 0.86$, see Table V for heritability estimate).

DISCUSSION

While the full sib analysis revealed genetic variance in the male leg rubbing behavior, the narrow sense heritability was very low and far from significant. This has implications for the evolution and maintenance of the female preference for males with vigorous copulatory courtship behavior, which we will discuss below.

Leg Rubbing as an Indicator of Viability

Although “condition” is clearly a central current concept in behavioral ecology (Bakker, 1999; Rowe and Houle, 1996; Tomkins *et al.*, 2004), it is unclear exactly how condition is best quantified in empirical studies (Arnqvist and Thornhill, 1998). One possibility is to assess to what extent male genotypes differ in their ability to withstand harsh environmental conditions (i.e., genotype \times environment interactions) (Arnqvist and Thornhill, 1998; Bjorksten *et al.*, 2000; Tomkins *et al.*, 2004), which amounts to testing whether condition dependent expression of traits is heritable (Grafen, 1990). Our experiments allowed us to test whether copulatory courtship behavior of

Table V. Heritabilities and their Standard Errors Calculated from Parent–Offspring Regressions

Trait	h^2	SE
Time until mating	-0.060	0.216
Copulation duration	-0.308	0.368
Rate of leg rubbing	-0.064	0.346

males can reveal individual condition and quality in this manner.

We did find a significant effect of sire on offspring survival (Table II). Hence, assuming that egg to adult survival is correlated with fitness, female *T. castaneum* could potentially gain indirect genetic benefits by preferring males with a trait indicating the possession of “good survival genes”. The rate of leg rubbing also showed significant repeatability among sires (Table I) and sire had a marginally significant effect on the rate of leg rubbing of offspring in the full sib analysis (Table IV). The effect of male genotype on offspring leg rubbing behavior, however, depended on which density treatment they had been reared in: the interaction between sire and treatment was significant (Table IV). Taken together, these analyses indicate that there is genetic variation in rate of leg rubbing in our population and that the expression of this behavior depends on the environment encountered by larvae. The relatively low availability of resources in the high-density treatment appeared to affect larvae since mortality was significantly higher here than in the low-density treatment. Beetles reared under high-density conditions should therefore be of worse condition than their siblings raised under low-density conditions.

Contrary to what might be expected, however, males reared in the low-density treatment did not show a higher average rate of leg rubbing than did males reared in the high-density treatment (Table IV, Fig. 1). Therefore, it appears that the expression of the leg rubbing behavior is not condition dependent in the sense that individuals in better phenotypic condition have a higher rate of leg rubbing. This is in line with the results of Pai and Yan (2003) who failed to find a significant effect of tapeworm infection on male leg rubbing in *T. castaneum* in spite of an apparent effect on male vigor. Most importantly, there was no relationship between rate of leg rubbing in sires and offspring survival in our study. The genetic variances in offspring survival and rate of leg rubbing were independent of each other and should therefore involve different sets of genes. In summary, this suggests that copulatory courtship behavior is of little or no use to females as an indicator of genetic qualities in males that affect offspring survival.

Heritability of Leg Rubbing

Although the full sib analysis showed marginally significant genetic variance in the leg rubbing behavior, the narrow sense heritability, estimated through

parent–offspring regression, was far from significant. Full sib analysis captures total genetic variance including the additive, dominance and epistatic components whereas a parent–offspring regression only estimates the proportion of the phenotypic variance made up of additive genetic variance (Falconer and Mackay, 1996). Therefore, the genetic variance in rate of leg rubbing indicated in the full sib analysis is most likely due to dominance variance and/or epistatic variance. This implies that females cannot increase the attractiveness of their male offspring significantly by using the sperm from mates with vigorous copulatory courtship behavior since sons of these males do not inherit their fathers’ high rate of leg rubbing. Female *T. castaneum* are often highly promiscuous and although other studies have found that they may increase the reproductive success of their sons by being polyandrous, whether the leg rubbing behavior plays a role in this or not is not known (Bernasconi and Keller, 2001; Pai and Yan, 2002).

Collectively, our results suggest that female *T. castaneum* cannot gain appreciable indirect genetic benefits by favoring males with a high rate of leg rubbing in our study population. The sons of preferred males are not more viable or have a more attractive copulatory courtship behavior than other males. However, we did not measure lifetime fitness of the offspring and our power to detect small additive genetic variance in the leg rubbing behavior was limited due to a moderate sample size and a relatively large standard error of the mean. Therefore, we cannot entirely rule out that females gain indirect benefits through fitness components not measured in this study and/or that there is some additive genetic variance in the leg rubbing behavior that could be detected by a larger study with higher statistical power. However, additive genetic variance in a male trait and indirect genetic benefits to choosy females are not necessary for a female preference for the male trait in question to evolve and be maintained. According to the sensory exploitation hypothesis, female preferences are side effects of female sensory or neural characteristics, which male traits evolve to exploit (see Ryan, 1998, for a review). Córdoba-Aguilar (1999) and Sakaluk (2000) have both suggested that male insects can use sensory exploitation to influence cryptic female choice. Males of the damselfly *Calopteryx haemorrhoidalis asturica* mimic the stimulus from an egg passing through the female reproductive tract with their genitalia to trigger the release of rival sperm, which is then removed (Córdoba-Aguilar, 1999). Sakaluk (2000) showed that nuptial food gifts

in crickets may have evolved to exploit the females' gustatory response and make them accept more sperm from an attached spermatophore than they would in the absence of a food gift. The male copulatory courtship behavior in *T. castaneum* may have evolved to exploit a bias in the female sensory system in an analogous way. If sensory exploitation has driven the evolution of male leg rubbing, then indirect genetic benefits to females are not necessary to maintain the female preference for this behavior as long as the preference is not costly for females (Ryan, 1998).

Time until Mating

We found a marginally significant effect of sire on offspring time until mating in the full sib analysis and also a marginally significant interaction with treatment. However, as for rate of leg rubbing, narrow sense heritability was very low and far from significant. Again, this indicates that there may be some dominance and/or epistatic variance in this trait and that its expression depends on the environmental conditions (Fig. 1). Similar to the expression of rate of leg rubbing, beetles reared in the high-density treatment did not show a longer time until mating than did beetles reared in the low-density treatment suggesting that individuals of better condition were not quicker to achieve matings.

In all, our results suggest that female *T. castaneum* do not gain any appreciable indirect genetic benefits by preferring males with intense copulatory courtship behavior. The sons of preferred males are neither more viable nor more attractive than other males. There is genetic variance in the leg rubbing behavior but it is independent of the genetic variance in viability and not condition dependent in its expression. Therefore, it cannot serve as indicator of "good viability genes". Furthermore, the genetic variance in the leg rubbing behavior appears to be mostly non-additive and consequently, sons of males with a high rate of leg rubbing do not inherit their fathers' intense copulatory courtship.

ACKNOWLEDGMENTS

We thank three anonymous reviewers for valuable comments and the Swedish Research Council for financial support.

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Edited by Yong-Kyu Kim