Copulatory courtship signals male genetic quality in cucumber beetles

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In the spotted cucumber beetle, *Diabrotica undecimpunctata howardi* (Coleoptera: Chrysomelidae), males court females during copulation by stroking them with their antennae. Stroking occurs exclusively during the first stages of copulation, after a male has penetrated a female's vaginal duct but before he is allowed access to her bursa copulatrix. Females accept the spermatophore of fast-stroking males and reject those of slow-stroking males by relaxing or constricting muscles distorting the vaginal duct. Here, we measure the repeatability of stroking behaviour within males, examine the effect of losing one antenna on male attractiveness and test whether such female control results in direct phenotypic benefits for the discriminating female or indirect genetic benefits that appear in her offspring. We also use a half-sibling design to quantify the variance and heritability of stroking speed and endurance. Female beetles were paired with a male that was known to stroke either quickly or slowly. No difference was found in the resulting fecundity or egg-hatching rate of the females, or in the survivorship, development rate, size, age at first reproduction or fecundity of their offspring indicating that no direct benefits are gained by discriminating among males on the basis of stroking speed. There were, however, good-genes benefits for the mates of fast-stroking males. Offspring of fast-stroking fathers were also fast strokers and were more likely to be accepted as mates than offspring of slow-stroking fathers. There was substantial variance among sires in stroking speed and endurance and the heritability of each trait was high. The antennal stroking rate was highly repeatable in successive mating attempts and males with only one antenna were not accepted as mates. The repeatability within males, variability between males and heritability between generations of copulatory stroking combine to provide females with a reliable and honest signal of the genetic quality of courting males.

Keywords: Chrysomelidae; good genes; copulatory courtship; sexual selection; female choice; spotted cucumber beetle

1. INTRODUCTION

Although the consequences of female choice are the same whether they occur before, during or after intromission, the importance of discrimination after intromission has been underappreciated in the past. Recent reviews present compelling evidence that females of many species can refuse, manipulate or reject male seminal products in more than 20 different ways after copulation has begun (Eberhard 1996, 1997; Hellriegel & Ward 1998). It is proposed that female control over the final stages of mating has driven the evolution of a diverse array of male courtship behaviours that are employed during or even after intromission, presumably to coax females into accepting and using the suitor's sperm to inseminate eggs (Wcislo *et al.* 1992; Eberhard 1993; Otronen 1994). In arthropods much copulatory courtship is comprised of behaviours such as tapping, stroking or rubbing that may require little in the way of energy expenditure. Whether copulatory courtship can provide females with honest signals of male quality has not, to our knowledge, been previously demon-

strated. Two types of benefits may result from female choice that is exercised after copulation has been initiated; direct phenotypic gains from seminal products or other nuptial gifts laden with nutrients or defensive chemicals (Thornhill 1983; LaMunyon & Eisner 1993), or indirect genetic benefits in the form of genes promoting the attractiveness or viability of offspring. Here, we present evidence that copulatory courtship conveys an honest signal to discriminating females about the genetic quality of courting males.

Diabrotica undecimpunctata howardi Barber, the spotted cucumber beetle (SCB), is a nearctic member of the Luperini, a tribe of galerucine chrysomelid beetles comprised of more than 3950 species (Wilcox 1972*a,b*). There is no evidence for any precopulatory male courtship or female choice in the SCB, although females signal receptivity and thus control the timing of male advances by releasing a sex pheromone (Guss *et al.* 1983). Males approach females from behind and quickly mount. The male clasps the lateral edges of the female's elytra with his first and second pair of legs, while his hind legs are extended behind to serve as stabilizers. Females typically attempt to dislodge males before penetration by bucking, kicking or rubbing against the substrate but are usually
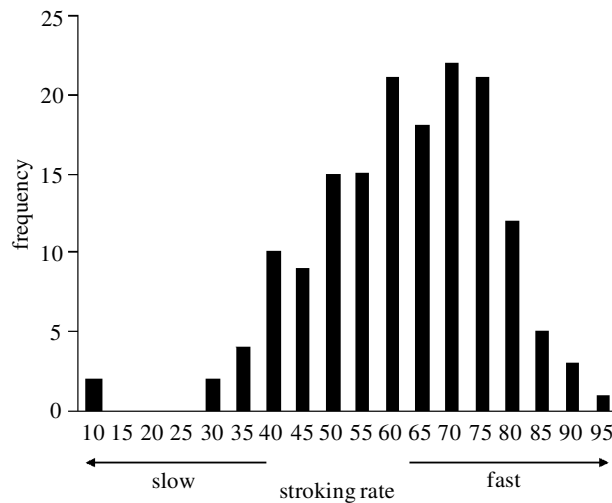
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Figure 1. The frequency distribution of copulatory antennal stroking in the population of SCB males from which the fast ($\geqslant 60$ strokes min^{-1}) and slow ($\leqslant 45$ strokes min^{-1}) rates were derived ($\bar{x} = 63.9 \pm 1.2$ s.e.).

unsuccessful in this endeavour. As soon as a male has secured his position he begins to probe with his aedeagus (penis) and often achieves partial intromission within seconds. Simultaneously he begins a rhythmical behaviour with his antennae that we call stroking; by quickly shaking his head three times from side to side while his antennae project forward and downward, a courting male strokes the lateral edges of the female's antennae, eyes and front legs. The dissections of beetles that have been flash frozen in supercooled ethanol have shown that males in copula repeatedly stroke until the female relaxes her vaginal duct muscles. This straightens the vaginal duct, which is otherwise pulled into an s-shaped curve, permitting access to her bursa copulatrix (Tallamy *et al.* 2002). A male that gains access immediately stops stroking, angles both antennae posteriorly over his elytra, and slowly pulsates his abdomen as he transfers a liquid spermatophore.

Female discrimination among males in copula is obvious in the SCB and can be recognized in any of three ways: the successful transfer of a complete spermatophore can be assessed by the direct dissection of the female's bursa post-copulation; by measuring the weight change (*ca.* 7% of total body mass; Tallamy *et al.* 2000) that occurs in both the male donor and the female recipient during copulation; or simply by observing if and when males stop stroking and hold their antennae motionless over their elytra. Males are rejected (fail to pass a measurable portion of their spermatophore) in 55% of all copulations (Tallamy *et al.* 2000). Preliminary unpublished data (D. W. Tallamy) indicate that some rejected males succeed in transferring small numbers of sperm. Whether females are capable of discriminating against these sperm is not known. Although SCB females only accept a complete spermatophore once in their lives, they will copulate with up to 15 males before doing so (Tallamy *et al.* 2000). Thus, SCB females have ample opportunity to evaluate male quality before accepting sperm. Here, we measure

(i) the degree to which male antennal stroking effects such evaluations;

(ii) whether females would benefit from discriminating among males solely on the basis of antennal stroking rate; and
(iii) the heritability of stroking rate.

2. MATERIAL AND METHODS

The beetle colonies used in these studies were derived from a squash field in Newark, DE, USA and were reared on corn roots as per Tallamy *et al.* (1997). The average period of copulatory courtship required to elicit female acceptance was measured by pairing 103 virgin males and females in plastic cups (4 cm in diameter) equipped with two small sticks to provide females with a substrate for dislodging males if they chose to do so. The time elapsed before males in copula stopped antennal stroking (acceptance) or until rejected males dismounted was recorded.

As part of our effort to determine the importance of antennal behaviour during courtship, we examined the effect of antennal ablation on male-mating success in two groups of males that had previously been accepted as mates during their first copulation. In the first group ($n = 15$), the flagellum from the left antenna of each male was snipped off with dissecting scissors. To inflict similar surgical trauma, the left maxillary palp was removed from males of the second group ($n = 14$). One day after surgery both groups were paired with virgin females and their percentage acceptance was recorded.

The antennal stroking rates were quantified by video recordings with virgin beetles (males 7–10 days old and females 3–7 days old) that were paired in test-tubes. Stroking rates are temperature dependent so all recordings were made at 23 ± 1 °C. To determine whether the 'accepted' males (i.e. judged by the females to be acceptable mates) stroke females differently to the 'rejected' males (i.e. those rejected by the females), 37 virgin males and females were paired and video taped during copulation. The stroking rate (antennal strokes per minute during the first 5 min of intromission) and the stroking endurance (stroke number during the first minute of intromission minus stroke number during the fifth minute of intromission) were compared between accepted ($n = 21$) and rejected ($n = 16$) males by *t*-test. We restricted our stroking measurements to the first 5 min of intromission for two reasons. First, females often accept their mates in less than 5 min and we did not want to bias our measurements against males that were particularly attractive by only quantifying males that were evaluated for longer periods. Furthermore, the stroking speed slows over time (Tallamy *et al.* 2002) making it difficult to accurately extrapolate stroking rate beyond that actually measured for beetles that are accepted quickly.

Evidence that antennal courtship behaviour is a trait that could be used by females to assess male quality was also found in measures of its repeatability within males over successive mating attempts. Repeatability quantifies the proportion of total phenotypic variance in a trait that is due to consistent differences among individuals rather than within individuals (Lynch & Walsh 1998). Ranging from zero to one, the repeatability (r) of a quantitative trait is estimated by making repeated measures of the trait on a sample of individuals and then calculating the ratio of the among-individual variance to the sum of the among-individual and within-individual variance as estimated from the mean squares of a one-way ANOVA (Lessells & Boag 1987). We measured repeatability (r) of the SCB stroking rate (mean antennal strokes per minute during the first 5 min of copulation) in virgin 8 day old males and then again one week later.

Table 1. Direct phenotypic effects ($x \pm$ s.e.) on females mated to males with fast or slow antennal stroking rates.

	male stroking speed			
fitness trait	fast	slow	statistic	p
no. of eggs during first 45 days	365.3 ± 49.1 ($n = 24$)	440.8 ± 65.2 ($n = 22$)	$t_{44} = 0.93$	0.3552
hatching (%)	67.2 ± 6.6 ($n = 28$)	74.8 ± 8.8 ($n = 20$)	$t_{41} = 0.70$	0.4875

Table 2. Indirect genetic effects ($x \pm$ s.e.) on offspring with fast- or slow-stroking fathers.

	father's stroking speed			
offspring trait	fast	slow	statistic	p
male stroke rate (strokes min^{-1})	72.5 ± 0.9 ($n = 38$)	56.7 ± 1.7 ($n = 29$)	$F_{1,22.3} = 74.85$	0.0001
probability of acceptance (%)	47.4 ($n = 8$)	20.7% ($n = 29$)	$\chi^2 = 6.0$	< 0.05
survivorship to adult (%)	19.1 ± 3.2	11.6 ± 1.9		
	24 cohorts	22 cohorts	$F_{1,36.2} = 4.05$	0.0517
days to maturity				
males	33.0 ± 0.6	31.9 ± 0.7	$F_{1,36.4} = 2.13$	0.1526
females	33.1 ± 0.6	34.0 ± 0.8	$F_{1,23.2} = 0.18$	0.6747
prothorax length (mm)				
males	1.12 ± 0.01 ($n = 84$)	1.14 ± 0.02 ($n = 64$)	$F_{1,20.7} = 0.94$	0.3437
females	1.18 ± 0.02 ($n = 55$)	1.15 ± 0.02 ($n = 31$)	$F_{1,30.7} = 1.40$	0.2460
age at first reproduction (days)	12.7 ± 0.7 ($n = 80$)	13.7 ± 0.9 ($n = 39$)	$F_{1,78} = 0.78$	0.3809
fecundity	330.8 ± 26.8 ($n = 92$)	389.2 ± 51.1 ($n = 41$)	$F_{1,8.2} = 0.99$	0.3336

To estimate the direct and indirect consequences of female preference, 5 min antennation rates (mean strokes per minute) were quantified in 160 virgin male offspring of field-collected beetles. We retained two groups of males (figure 1); 'fast' males ($n = 24$) that showed high rates (mean $\pm$ s.e. $= 79.3 \pm 16.2$) and 'slow' males ($n = 25$) with much lower rates (38.6 ± 8.2). Males that met the criteria for fast and slow treatments were each permanently paired with a virgin female at 24 °C. The effect of possible nutrient gifts from males to females was assessed by measuring differences in fecundity for 45 days and egg-hatching rates (percentage hatched after 7 days at 27 °C) between mates of slow and fast males. To quantify genetic benefits associated with accepting sperm from fast or slow males, larvae from the first 50 eggs produced by each female in both treatments were reared blind to their father's stroking rate in 4 oz plastic cups on corn roots in potting soil. As superior genotypes may not be measurably apparent within stress-free environments, larvae were reared under stress from competition for limited food (roots from only 20 corn seedlings per rearing cup). For both treatments we quantified the percentage larval survivorship per rearing cup, maturation time (days from egg hatch to adult eclosion) and body size (prothorax length) of each adult that emerged. The fecundity of female offspring was also quantified, as was the attractiveness of male offspring by video taping copulation as before, recording the stroking and acceptance rates during the first 5 min of copulation. As some males produced more surviving offspring than others, the design was unbalanced and was consequently analysed with a Satterthwaite approximate *F*-test (Satterthwaite 1946) with fathers nested within treatments.

(a) *Genetic analysis*

Using a paternal half-sibling breeding design (Lynch & Walsh 1998) we estimated the narrow sense heritablility of stroking speed and stroking endurance by respectively analysing the number of strokes during the first minute of intromission and the average strokes per minute after 5 min of intromission. Virgin males and females were chosen randomly from the offspring pool of over 100 field-collected SCB females. Beginning 5 days after eclosion, 40 males were each mated to five 3-day-old females with 2 days between each mating. Previous work has shown that this is more than enough time for males to produce a new full-sized spermatophore (Tallamy *et al.* 2000). Each female's offspring was reared on corn roots in styrofoam cups. The position of each cup on benches was randomized daily to minimize the covariance of family and possible environmental effects. As adults eclosed, they were separated by sex, and males were held for 5 days. The stroking speed and endurance of five males from each family were then quantified as before.

Variance components were estimated from a nested ANOVA using the model $Y_{ijk} = \mu + \alpha_i + \beta_{ij} + e_{ijk}$ where μ is the mean, α_i is the effect of the ith sire, β_{ij} is the effect of the jth dam mated to the ith sire, and e_{ijk} is any environmental and genetic variance associated with individuals (Lynch & Walsh 1998). Owing to occasional imbalances in the number of dams per sire or the number of sons per dam, heritability standard errors were calculated following equations suggested by Lynch & Walsh (1998) for unbalanced designs. Significance was tested with Satterthwaite's approximation (Satterthwaite 1946).

3. RESULTS AND DISCUSSION

Data from each of our experiments indicate that copulatory antennal stroking is a trait that is either directly used by SCB females or is correlated with a trait such as immunocompetency that enables females to evaluate the genetic quality of male suitors. A female's decision to

Table 3. ANOVA table with variance components estimated from a nested full-sibling–half-sibling analysis of the antennal stroking rate after 1 and 5 min of coupling.

	1 min				5 min			
source	d.f.	MS	variance	p-value[a]	d.f.	MS	variance	p-value[a]
sires	39	765.31	25.93	< 0.0001	39	504.81	14.16	0.0002
dams	139	244.89	26.05	< 0.0001	138	230.51	24.30	< 0.0001
error (sons)	723	115.12	115.12		694	112.78	112.77	

[a] Satterthwaite approximate F-tests.

accept or reject a suitor is usually made within the first 30 min of copulatory courtship (29 ± 5 min; $n = 73$), but rejected males continue to stroke females at a progressively slower rate, sometimes up to 8 h (154 ± 31 min; $n = 30$) before giving up and dismounting. Acceptance does not depend on male weight, male : female weight ratio, aedeagus length or the load of sequestered chemical defences (Tallamy *et al*. 2002). Males that are accepted as mates ($n = 21$), however, stroke at a significantly faster rate (accepted males = 50.9 ± 1.9 strokes min^{-1}; rejected males = 33.8 ± 2.8 strokes min^{-1}; t-test; $t = 5.23$; $p < 0.0001$) and with significantly more endurance (rate of decline for accepted males = 4.2 ± 1.1 strokes min^{-1}; for rejected males = 9.9 ± 2.5 strokes min^{-1}; $t = -2.07$; $p = 0.0511$) than do rejected males ($n = 16$). Furthermore, males from which the flagellum of one antenna was surgically removed were never accepted as mates, while 48% of males with both antennae left intact were accepted by the first female they approached. We did not measure the effect of removing one antenna on the stroking speed of the remaining antenna but this simple experiment indicates that full and perhaps symmetrical antennal movement is required for successful SCB courtship. Finally, we found that antennal stroking was highly repeatable within males over successive mating attempts ($r = 0.97$; $F_{1,29} = 57.2$; $p = 0.0001$) and yet highly variable among males, ranging from 21 to 94 strokes min^{-1} (s.d. = 16.3) at 27 °C. That is, fast males are always fast and slow males are always slow; thus, antennal stroking behaviour could serve as a consistently accurate index of male quality if it is directly or indirectly correlated with male traits that elevate female fitness.

We found no evidence that females who select mates on the basis of male antennal stroking behaviour benefit phenotypically from such discrimination. Females paired with either the fastest ($\geqslant 60$ strokes min^{-1}) or the slowest ($\leqslant 45$ strokes min^{-1}) males in the population did not differ in fecundity or egg viability (table 1) nor did they produce offspring that developed faster, reproduced sooner, were larger or were more fecund (table 2). There are other traits such as female lifespan or the ability to escape predators that could conceivably benefit from nuptial gifts borne by fast males but it is improbable that the spermatophores of fast-stroking males could be qualitatively or quantitatively superior to those of slow strokers in their content of nutrients or hormones without affecting at least one of the traits we did measure. Furthermore, we know from previous work that there is no relationship between stroking rate and male size, spermatophore size or the

quantity of sequestered secondary metabolites (i.e. cucurbitacins) (Tallamy *et al*. 2002). SCB spermatophores seem to be largely comprised aqueous material that fills a female's bursa (regardless of the male's size or the size of the female's bursa), pushing a well-defined sperm sac into the anterior end of the bursa adjacent to the entrance to the spermathecal duct.

Similarly, we found no evidence that females differentially allocated resources to eggs that were sired by fast and slow males. Females mated to slow-stroking males laid as many eggs as females mated to fast-stroking males and the eggs of both treatments had equal hatching success. Differential allocation has been noted in several polyandrous iteroparous organisms (Burley 1988; Sheldon 2000) but could not be adaptive in the SCB because females only accept the sperm of one male in their lifetime. If circumstances conspire to make that male a low-quality, slow-stroking male, it would not benefit a female to withhold resources from eggs sired by that male because he is destined to sire all of her eggs.

Although we found no direct phenotypic benefits associated with fast-stroking males, the data indicate that SCB females mated to fast strokers did receive indirect genetic benefits that were not passed to mates of slow males. Females with fast mates were significantly more likely to bear fast-stroking sons that, in turn, were significantly more likely to be accepted as mates (table 2). Half-sibling estimates of the heritablity of stroking rate after 1 min of coupling (0.62 ± 0.20), a measure of stroking speed, and after 5 min of coupling (0.37 ± 0.15), a measure of stroking endurance, were both highly significant (table 3). Despite the fact that SCB males provide no paternal care to offspring, it is possible that some of the observed similarities between the stroking behaviour of a father and his sons were the result of non-genetic paternal effects. The highly heritable nature of the early stages of copulatory stroking, however, ensures that SCB females who discriminate between potential mates on the basis of stroking behaviour receive 'good attractiveness genes' (Kirkpatrick 1996; Kirkpatrick & Barton 1997; Møller & Alatalo 1999) that improve the mating success of male offspring. Furthermore, there was a significant sire effect for both stroking speed and endurance, indicating that there is genetic variance in these courtship traits.

There was also some indication that the offspring of females with fast mates had a greater chance of surviving to adulthood than did the offspring of females with slow mates, at least under laboratory conditions (table 3). Laboratory demonstrations of 'good-viability genes' (Fisher

1930; Lande 1981; Kirkpatrick 1982) that enhance off-spring fitness are poor substitutes for comparable studies in the field because of the simplicity of the microcosm in which fitness is expressed. In our study food shortages that were deliberately introduced during larval development were most probably survived by larvae with genetically superior foraging, food assimilation or competitive abilities, as well as by larvae most resistant to stress-induced diseases. We recognize, however, that given the number of traits examined, it is entirely possible that the marginally better survivorship observed in larvae of fast-stroking males occurred by chance alone.

Genetic benefits have recently been demonstrated for females that select mates before copulation on the basis of fixed morphological traits (i.e. the ornamentation of crest (Sheldon *et al.* 1999) and tail feathers (Petrie 1994) in birds, the length of eye stalks in diopsid flies (Wilkinson *et al.* 1998) and the size of forceps in earwigs (Tomkins & Simmons 1999)); chemical cues signalling the complimentary nature of a male's immune system (Drickamer *et al.* 2000); and the quality of precopulatory behaviour (i.e. frog call duration (Welch *et al.* 1998) or *Drosophila* mating song pitch (Hoikkala *et al.* 1998)). The fact that genetic benefits are also conveyed to females who select mates via courtship performed while coupling confirms the prediction (Eberhard 1996) that traits comprising copulatory courtship are both widespread and are under selection from female preference. How male traits that signal good genes retain enough genetic variation to warrant female discrimination continues to generate debate (Pomiankowski & Møller 1995; Rowe & Houle 1996; Møller & Alatalo 1999; Widemo & Sæther 1999; Kotiaho *et al.* 2001).

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