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Mating Behavior, Sexual Selection, and Copulatory Courtship in a Promiscuous Beetle

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*The function of male movements during copulation is unclear. These movements may be a result of the necessary mechanics of insemination, or they may also have further function, for instance, stimulating or courting a female during mating, perhaps influencing female mate choice. We present data from three experiments exploring the mating behavior and copulatory movements of the highly promiscuous beetle *Psilothrix viridicoeruleus*. Male mating success in the struggle over mating was not related to male or female size (measured by weight) but successful males were more vigorous in terms of copulatory movements. These males took longer to mount females but copulated longer and remained mounted longer. We discuss these results in terms of the mating system of *Psilothrix* and also in terms of observations of the timing of insemination during copulation. We suggest that copulatory movements in this species are best understood as copulatory courtship.*

KEY WORDS: copulatory courtship; sperm competition; sexual selection; *Psilothrix*.

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INTRODUCTION

Traditionally courtship has been viewed as a set of precopulatory signals by which a male seeks to gain access to the female, presumably by satisfying a set of female choice criteria (Alexander *et al.*, 1997). However, there is growing evidence that males sometimes continue to court females during, and even after, copulation. In particular, the widespread occurrence of rhythmic or repeated movements by male insects during copulation has led to the suggestion that “copulatory courtship” may be an important, yet underreported, component of sexual selection in many groups (Eberhard, 1991, 1994, 1996). The reason copulatory courtship may be so important is that sexual competition need not end with mating. It has become clear that the number of matings obtained by a male often does not equate with fertilization success in species where females mate multiply (e.g., Reynolds, 1996; Birkhead and Møller, 1998). Sexual competition may continue after mating as competition between male ejaculates within the female reproductive tract [“sperm competition” (Parker, 1970)] or through females actively or passively favoring one male’s sperm over another [“cryptic female choice” Thornhill, 1983]. Male- and female-driven processes may interact, perhaps with males attempting to bias female utilization of sperm in their favor. Copulatory courtship has been put forward as just such a mechanism by which males influence cryptic female choice in polyandrous species (Eberhard, 1996).

However, the role of cryptic female choice and copulatory courtship has proved to be surprisingly controversial. There is still confusion over the nature of copulatory and postcopulatory interactions and whether they represent male- or female-driven processes or, indeed, whether they should be viewed as sexual conflicts between males and females over the control of fertilization (Alexander *et al.*, 1997; Eberhard, 1997; Brown *et al.*, 1997; Simmons and Siva-Jothy, 1998). For some species where well-recognized precopulatory courtship, such as singing, occurs during copulation, it is quite clear that courtship continues, or is indeed initiated, after the male and female have come together. For instance, both *Drosophila birchii* and *D. serrata* males produce song predominantly during copulation, and males prevented from doing so are more likely to be rejected by females before copulation is completed (Hoikkala and Crossley, 2000; Hoikkala *et al.*, 2000).

Movements that occur only during copulation are perhaps more difficult to interpret—Are they merely incidental movements associated with the correct positioning or functioning of the intromittent organ? For some copulatory movements, such as the “rocking” and “rolling” of the whole body by some male coccinellid beetles during mating (Majerus, 1994), perhaps a simple mechanistic explanation such as spermatophore construction

is sufficient (Ransford, 1997). For other movements, for instance, involving the antennae or forelegs, there appears to be little obvious association with internal positioning of the aedeagus. These movements are redundant unless they are indeed stimulatory to the female, allowing insemination to take place or encourage the storage and utilization of sperm (Eberhard, 1996). A recent study of *Tribolium castaneum* by Edvardsson and Arnqvist (2000) showed that male rubbing of the edges of the female elytra during copulation directly influenced the number of a male's sperm that fertilized a female's eggs, confirming the functional significance of these movements in this species. Finally, movements of the male genitalia within the female reproductive tract are also difficult to interpret, although they may again be stimulatory. For example, in the damselfly *Calopteryx haemorrhoidalis asturica* movement of the male aedeagus stimulates the female to release sperm from her spermatheca that can then be removed by the male and replaced with his own sperm (Córdoba-Aguilar, 2000). As a result there is the potential for sexual selection to act on male morphology and movement in this system.

To complement the few studies of copulatory courtship behavior conducted to date, this study considers the highly promiscuous beetle *Psilothrix viridicoeruleus* Geoffroy and describes its mating system and the often vigorous male mating behavior. We present data examining correlates of male mating success and explore the possibility of copulatory courtship in this species, addressing three questions. (1) Are male copulatory movements associated with aspects of mating success, such as the time taken to mount a female, time taken to engage genitalia, time in copula, and time mounted on a female? If male copulatory movements are a form of copulatory courtship, then we predict that variation in copulatory vigor is related to mating success and male–female behavioral interactions. For instance, we predict that males that perform a higher rate of copulatory movement are more likely to copulate. (2) Is male and female body size associated with differences in copulatory behavior and mating success? Here we examine whether body size is a target of sexual selection and related to copulatory behavior. Two experiments are described that quantify mating behavior and male mating success in two mating situations (one male and one female together for one mating interaction and one male and three females together for 6 h). (3) How is insemination associated with patterns of copulatory behavior? Here we predict that if copulatory movements are a form of courtship, then they will not be closely associated with processes such as insemination, instead continuing after insemination has terminated while sperm moves to the sperm storage organ. A third experiment is described that relates the timing of insemination to the patterns of copulatory behavior observed in the previous experiments.

METHODS

Study Organism and Study Site

Psilothrix viridicoeruleus (Coleoptera: Melyridae) is a small (5- to 7-mm) sexually dimorphic bright blue-green beetle, associated with flowering herbaceous plants. Males and females are easily sexed using differences in abdomen morphology. Adults were collected from the dune slacks at Praia do Rei, Costa da Caparica, approximately 10 km south of Lisbon, Portugal (March–April 1999). Field observations were also made at this site during this time. *Psilothrix* are found on a range of plant species, including *Carpobrotus edulis* and *Matthiola incana*, where they are very abundant. Mating experiments were conducted at the nearby Quinta de Sao Pedro experimental station, Sobreda. Observations feeding behavior and analysis of gut contents confirmed that adult *Psilothrix* are pollen-eaters. Larvae were not observed during our study, although *Psilothrix* larvae have been found within stems of herbaceous plants (Crowson, 1964). Observed behavior of females at flower heads is consistent with possible oviposition.

Male and female *Psilothrix* mate repeatedly in the field. Males attempt to mate with all females that come to feed or oviposit at flower heads, revisiting and mounting females that they have already mated with. Intriguingly, recently mated females are often dismounted without further copulation, although at one flower all females were remated at least twice in 2 h. Typically only one male is present on a flower head and incoming males tend to leave right away if they encounter another male. However, on *Carpobrotus*, which has quite large flowers (8–10 cm in diameter), more than one male may remain and copulate with the females present. Whether this system reflects male territoriality needs further study. These observations suggest that the mating system resembles resource-defense polygyny, at least in certain circumstances (Emlen and Oring, 1977).

Description of Copulation Behavior

The following description is drawn from observation made in the field and the laboratory. There appear to be no qualitative differences in copulatory behavior between the field and the laboratory, although quantitative data for the former have yet to be collected. Males approach and mount females with no courtship. Neither sex appears to respond to each other until at a very close range (10 mm or less). Males mount females from the rear and immediately perform a variety of movements while attempting to engage genitalia. These movements include (i) thrusts, where the whole male

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body is thrust forward; (ii) abdomen taps, where the male taps the middle region of the female's abdomen primarily with his midlegs; (iii) rear taps, where the male taps the end of the female's abdomen with his hind legs; (iv) antennal taps, where the male taps the female's head and antennae with his own antennae; and (v) head taps, where the male taps the female's head and thorax with his head. Having achieved intromission, males continue this suite of copulatory movements. Females attempt to resist mounting and intromission by running away, kicking, and shaking their bodies. These rejection responses can remove mounted males and prevent copulation. Males dismount following successful copulation, generally without further female rejection responses.

Collection and Husbandry

Adults were collected either by aspiration or by directly knocking beetles from flowers into plastic tubes. Collections were made throughout the study period to minimize the time individuals spent in captivity prior to experiments. In the laboratory, individuals were kept in plastic aquaria (30 × 20 × 20 cm) or petri dishes, with fresh *Oxalis* flowers as a food source and moist paper towels, at ambient temperature (24–28°C). All handling was carried out without anesthesia. All individuals were used in only one experiment and returned to the field as soon as possible afterward. Using wild-caught individuals we could not determine the mating status (virgin/nonvirgin) of individuals, and so to standardize recent mating experience prior to all the experiments we put groups of males and females together for approximately 6 h and allowed them to mate freely. Observations showed that all individuals mated at least once during this period. Individuals were then isolated for 24 h prior to experiments.

Laboratory Experiments

Experiment 1: Analysis of Copulatory Behavior

Fifty pairs of pseudo-randomly chosen males and females were placed in separate petri dishes and the time to the first male mount, time to genital engagement, copulation duration, and mount duration recorded. Observations were carried out at ambient temperature (24–28°C) and a fresh *Oxalis* flower was available in the petri dish. If pairs had no interactions in the first 30 min, the mating trial was terminated. Observations were made for 1 min, every 5 min, starting at minute 2 after interactions commenced. The

numbers of male thrusts, abdomen taps, rear taps, thorax taps, antennal taps, and head taps were recorded for each minute of observation and behavioral rates calculated. Pairs that were mounted for only 60 s or less were excluded, as they performed little sexual behavior, leaving 35 pairs with sufficient observations. An overall measure of courtship ("courtship index") was also calculated as the number of different copulatory movements performed during the trial (ranging from zero to six). An additional composite measure of courtship was explored, using a principal components analysis (PCA) of the six courtship components. However, these six behaviors were at best only weakly correlated with each other (Pearson's correlation, $r < 0.6$; only one correlation significant at the 5% level), making interpretation of the PCA results problematic, and this analysis is not included below. Five of the six components of courtship were significantly positively correlated with the courtship index (antennal tap rate, $r = 0.23$, $P = 0.18$; other components, $r = 0.36$ – 0.51 , $P < 0.03$), implying that this simple index is not biased by one or two of the behaviors. Following each mate trial, individuals were weighed with an electronic balance as a measurement of body size (although three males escaped before being weighed).

The relationship between male and female body size and mating success (whether the pair copulated or not) was analyzed with stepwise logistic regression, with significant terms included in the final model. Significance was assessed with likelihood ratio tests. The relationships between copulatory movements and aspects of the male–female interactions were studied with stepwise multiple regressions, again, with only significant terms included in the final models. All dependent variables were normally distributed (Kolmogorov–Smirnov tests; all NS). Male and female size was also included in the initial models to explore size effects. Both the logistic and multiple regressions and the other descriptive statistics were performed with SPSS 10 (SPSS Inc., 2000). Means are presented \pm standard deviation.

Experiment 2: Copulatory Behavior and Male Mating Success

Twelve males were placed in separate petri dishes along with three females and observed by scan sampling for 6 h. Whether a male was in the process of mounting a female was scored every 15 min, and if so, behavioral observations were made for 1 min. The copulatory movements recorded were restricted to thrusts and abdomen taps (identified by preliminary analysis of Experiment 1 as the most common movements). Thrust and abdomen tap rates were calculated as the number of thrusts or taps per minute mounted on a female. Again, these trials were performed at ambient temperature with fresh *Oxalis* flowers available. Two trials in which the

males failed to interact with any of the females within the first 60 min of the trial were terminated.

The associations among time mounted, time in copula, and copulatory movements were analyzed with Spearman's rank correlation (using SPSS 10), and again, means are presented \pm standard deviation.

Experiment 3: Timing of Insemination

Males and females were paired in petri dishes as before and copulation was interrupted at various points. Pairs were separated and the females immediately frozen at -10°C and dissected to determine whether they had been inseminated and where the sperm was located within each female. In total, 18 females were dissected, blind with respect to the timing of the interruption. Seven females were frozen and dissected without having copulated, four pairs were interrupted after 5 min of copulation, two pairs were interrupted after 10 min, two females were frozen at the end of copulation (genitalia disengaged; both copulations of more than 10-min duration), and three females were frozen and dissected following male dismount. Importantly, all females were nonvirgin prior to the 24 h in isolation before the experiment (see above).

RESULTS

Experiment 1: Analysis of Copulatory Behavior

There was significant sexual size dimorphism, with males weighing on average 8.06 ± 1.95 mg and females 9.27 ± 2.62 mg (t test: $t_{77} = 2.31$, $P = 0.02$). Male and female weights of pairs were not correlated (Pearson's correlation: $r = 0.18$, $P = 0.27$; $N = 38$). Table I details the descriptive statistics from Experiment 1. In total, 29 of the 41 pairs that attempted sexual activity copulated, giving a mating rate of 70.7%. Whether or not a pair mated was not associated with male or female weight (stepwise logistic regression; no significant terms in the model). The mean mount duration was approximately 26 min, with copulations lasting about 18 min. Importantly, the mean time taken to engage genitalia exceeded 7 min, and males often remained mounted to females after disengaging genitalia for several minutes before finally dismounting. The most common copulatory movements were thrusts (93% of mounts) and abdomen taps (72%), with antennal taps (66%) and head taps (52%) fairly frequent. Thorax and head taps were less common. The number of copulatory behaviors (courtship index) performed varied from zero to all six. For the two most common copulatory movements,

Table I. Descriptive Statistics from Experiment 1

	Mean	SD	<i>N</i>	Range
Copulation duration (min)	18.11	9.56	29	0.48–50.65
Time to mount (min)	4.36	5.64	35	0.30–20.67
Time to engage genitalia (min)	7.72	9.02	29	0.80–37.03
Mount duration (min)	25.98	17.95	35	1.35–75.45
Thrusts min ⁻¹	5.56	6.87	35	0–27.33
Abdomen taps min ⁻¹	4.51	7.74	35	0–39.25
Thorax taps min ⁻¹	0.13	0.31	35	0–1.20
Head taps min ⁻¹	0.44	0.61	35	0–2.20
Rear taps min ⁻¹	0.36	0.83	35	0–3.40
Antennal taps min ⁻¹	2.76	5.16	35	0–23.50

thrusts and abdomen taps, there were no differences in the timing of the behaviors, with both occurring frequently throughout mating interactions (data not shown).

For the stepwise multiple regression we restricted the analyses to the most common behaviors, namely, thrusts per minute, abdomen taps per minute, antennal taps per minute, and courtship index. We included male and female body weights in the regressions as well, to control for any size effects. Thrust rate was the only significant variable remaining in the regression model, with time to mount as the dependent variable (regression coefficient, $\beta = 17.8$; $P = 0.04$). The positive regression coefficient means that males that thrust more vigorously once mounted took longer to mount in the first place. The time taken to engage genitalia, which varied quite considerably, from 5 s to 37 min (Table I), was not related to any of the variables in the model. With copulation duration as the dependent variable both courtship index and thrusts per minute were significant variables in the final regression model ($\beta = 208.8$ and 28.7 , $P = 0.006$ and 0.03 , respectively; Figs. 1a and b). Courtship index was the only significant independent variable in the regression model, with mount duration as the dependent variable ($\beta = 409.9$, $P < 0.001$; Fig. 2). Therefore the durations of both copulations and mounts were strongly associated with the range of courtship behaviors performed, with male thrust rate also playing a role.

Experiment 2: Copulatory Behavior and Male Mating Success

The mean male weight was 8.41 ± 2.18 mg in this experiment. The mean number of abdomen taps per minute mounted performed by the males was 2.60 ± 2.47 (range = 0.20–8.46), and the mean number of thrusts per minute mounted was 2.12 ± 1.75 (range = 0.00–5.46). On average, males spent 55% of sample units mounted on one of the three females (range = 21–92%,

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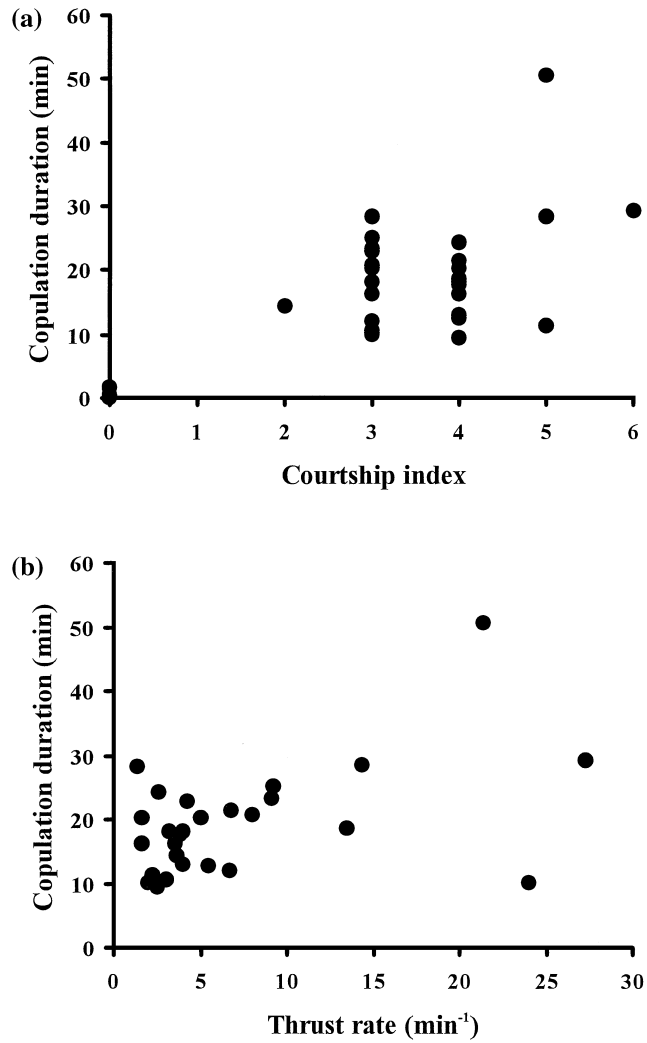


Fig. 1. The relationship between copulation duration (min) and (a) courtship index and (b) thrust rate (min^{-1}). Data are from observations for 1 min, every 5 min, until the male dismounted the female (Experiment 1).

5–22 sample units) and 18% of sample units in copula (range = 4–29%, 1–7 sample units). There was no significant correlation between the male weight and either the number of times a male was mounted on a female or the number of times a male was in copula [Spearman's rank correlation:

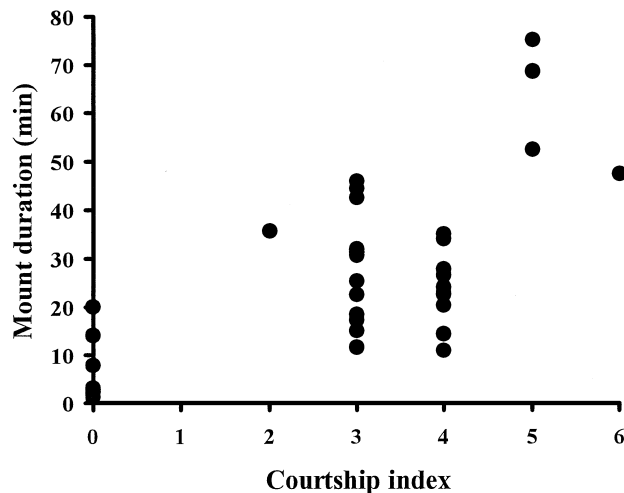


Fig. 2. The relationship between courtship index and mount duration (min). Data are from observations for 1 min, every 5 min, until the male dismounted the female (Experiment 1).

$r_s = -0.08$ and 0.00 ($P > 0.8$), respectively]. There was also no correlation between male weight and tap rate or between male weight and thrust rate ($r_s = -0.20$ and -0.04 , $P > 0.5$, respectively), although tap rate and thrust rate were themselves significantly positively correlated ($r_s = 0.71$, $P = 0.02$). Again, male size appears to have little association with mating success or frequency of copulatory movements. Finally, there were significant positive correlations between the number of times a male was in copula and both thrust rate and tap rate [thrust rate, $r_s = 0.81$, $P = 0.004$ (Fig. 3a); tap rate, $r_s = 0.75$, $P = 0.01$ (Fig. 3b)]. This clearly indicates that males that are more vigorous while mounted had greater mating success, copulating more frequently and/or for longer.

Experiment 3: Timing of Insemination

All seven females that were dissected without copulating (0 min) had sperm present in the spermatheca (sperm storage organ) but not in the bursa copulatrix (where sperm is deposited by the male). This suggests that the spermatheca is the primary sperm store and that bursal sperm that do not move to the spermatheca are lost over time, either passively or through active expulsion by the female. It proved impossible to separate pairs after 5 min of copulation without eviscerating the male and/or female, and so for these four pairs both male and female were frozen. Presumably the inflation

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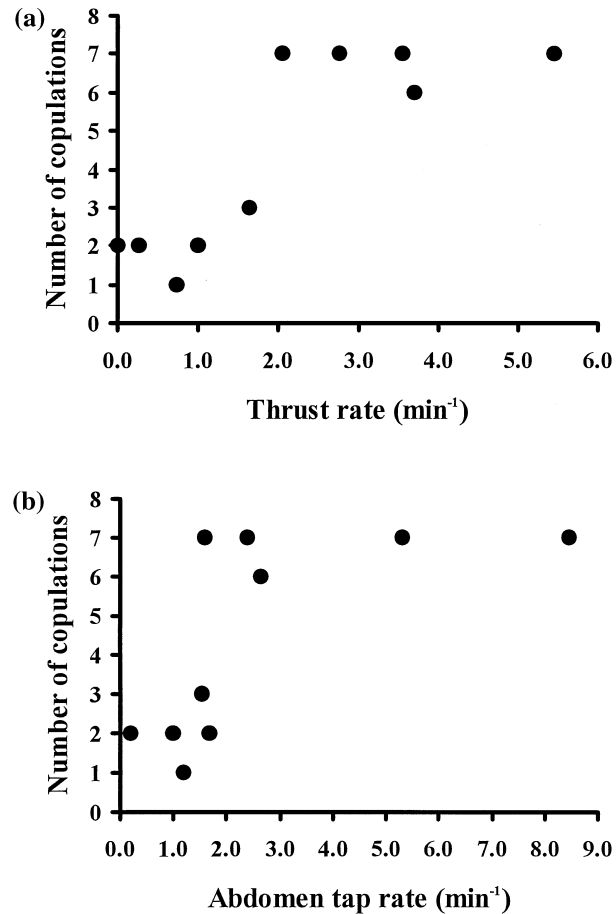


Fig. 3. The correlation between number of copulations and (a) thrust rate (min^{-1}) and (b) abdomen tap rate (min^{-1}). Data are from observations for 1 min, every 15 min, for 6 h (Experiment 2).

or positioning of part of the male aedeagus prevented withdrawal during this stage. Dissections of these pairs proved difficult, and while sperm was present in the spermathecae of all four females, it was not clear whether insemination into the bursa copulatrix had commenced by this stage. After 10 min, however, pairs could be separated even though the genitalia were fully engaged, suggesting a different phase of copulation, perhaps postinsemination, from that occurring at around 5 min. Both females had sperm present in the bursa at this stage, although one female had no traceable sperm in her spermatheca. Both females dissected at the end of the copulation (following genitalic

disengagement) had sperm in the bursa and spermatheca, and the size of the sperm mass was similar to that noted after 10 min, although no count of sperm numbers was made. Of the three females dissected after the male had dismounted voluntarily, two had sperm in the bursa and spermatheca, while one just had sperm in the spermatheca, suggestive of a failed insemination attempt by that male. In summary, these observations suggest that copulation in *Psilothrix* involves at least two phases: the first, in which the male intromittant organ is firmly locked in the female's reproductive tract and possibly when insemination takes place; the second, in which the male genitalia can be removed easily from the female and by which time insemination appears to have been completed. The first phase is complete within 10 min and that copulation proceeds for longer than is necessary merely to transfer sperm.

DISCUSSION

It is clear that there are distinct male movements that occur during copulation in *Psilothrix*. Males employ a number of parts of their body to touch and tap females, often quite vigorously, throughout the mating interaction, and males vary in the number of different behaviors they perform and the extent of these movements. In the first two experiments, this variation in copulatory movements of males is associated with aspects of the mating interaction and with measures of mating success, in particular, the number of copulations obtained by a male. These associations are what we would predict if such movements during copulation function as a form courtship and are not just ancillary movements associated with the mechanics of mounting and inseminating females. How convincingly do our data imply that copulatory courtship occurs in this beetle?

Taken together, the three experiments show that male copulatory movements continue after insemination, and so it is unlikely that they are just incidental consequences of moving or positioning the genitalia. The fact that males remained mounted after the genitalia have disengaged, and continue to perform these movements, is again indicative that copulatory movements are not wholly associated with the mechanical necessities of copulation. It is also unlikely that movements of the male antennae, for example, could relate to internal positioning or functioning of the aedeagus (see also Eberhard, 1996). However, not all male movements need necessarily share the same function (or lack of function) and some may be associated with the mechanics of insemination to different degrees. In terms of mating success in our experiments, male thrusting was the most important individual behavior performed, with some other behaviors by themselves being less important. Does this mean that the latter movements have only a primary function

sexual function? If this were the case, then we would predict that all males would have to exhibit each of the behaviors, albeit briefly, during copulation and insemination, and this was not observed. Instead, the data suggest that the repertoire of a male is important, with males that perform more behaviors being more successful in terms of two of our measures of success in Experiment 1 (copulation duration and mount duration). That males are attempting to signal to or stimulate females with at least some of their copulatory movements seems the most plausible conclusion.

There is the possibility that the prolonged postinsemination interactions represent a form of postcopulatory mate guarding (e.g., Alcock, 1994). Considering our observations that sperm are placed in the bursa copulatrix and probably need to reach the spermatheca to remain in storage (since no sperm was seen in the bursa 24 h after copulation, only in the spermatheca), males have to ensure that females do not mate with another male until their sperm have reached the spermatheca. This guarding would be more efficient if females are stimulated to store the male sperm through copulatory courtship. Prolonged male–female interactions could act both as guarding by the male and as a more direct means of improving the chances that his sperm are stored and then utilized.

The considerable variation in time taken to engage genitalia and start copulating once mounted is interesting since we may expect courting males to balance the length of courtship with the risks of being interrupted, perhaps by another male or a predator. However, we found no relationship between any of the courtship variables and the time taken to engage genitalia. It is not clear which sex determines when intromission occurs and we controlled for other factors such as male density and male–male contest competition for females in these laboratory experiments. Variation in the length of courtship would seem to be an obvious target of selection if these movements do influence female choice in any way and merits closer scrutiny.

If male movements are not due to the mechanics of insemination, are there any other hypotheses that may explain these movements apart from courtship? One alternative hypothesis for copulatory movements that may be relevant involves the marking of females by males during copulation (Eberhard, 1996). It has been suggested that contact between males and females may involve the passing of pheromones, presumably as a form of antiaphrodisiac. In *Psilothrix*, the head tap behavior is the most likely candidate for such a marking function, with male mouthparts and antennae coming in contact with the female head and thorax. If this is the case, we predict that mount durations would be bimodal (either very short, when a male encountered an antiaphrodisiac, or long enough to include copulation) and that marking behaviors would be very common. We do not have the data to test this first prediction thoroughly at present, but the distribution of

mount durations was not significantly different from a normal distribution (Kolmogorov–Smirnov test, $P = 0.9$). In addition, we did not see head taps occurring as frequently as we might expect if they function to sense or leave a mark. However, it is worth remembering that the females, although not virgin, had not been in contact with males for at least 24 h, so any pheromonal markings may have dissipated. Observations in the field indicate that males recognize very recently mated females, indicative of pheromone marking. These markings need not be for other individuals, but only for the marking male, to keep track of recently visited females. Individual marks have recently been demonstrated in the solitary bee *Anthophora plumipes* in the context of foraging (Gilbert *et al.*, 2001).

Finally, although not the main concern of this present study, our data indicate no sexual selection on male or female size in terms of mating success. The sexual size dimorphism apparent in *Psilothrix* is perhaps best considered in terms of differences between the sexes in natural selection on body size, selecting for larger females, rather than sexual selection. The common positive relationship between size and fecundity in female insects is a plausible basis for this difference.

Male copulatory behaviors, which are remarkably widespread among insects and arachnids (Eberhard, 1991, 1994), are in need of a satisfactory explanation. We propose that our observations of male copulatory movements in *Psilothrix* suggest copulatory courtship and suggest that this species provides an ideal candidate for the study of the processes of copulatory and postcopulatory sexual selection and the functional significance of these intriguing male copulatory movements.

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