Post-copulatory mate guarding in decorated crickets

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Abstract. Although post-copulatory mate guarding occurs in a variety of crickets, its adaptive significance remains largely unknown. Mate guarding may function to prevent females from prematurely removing the externally attached sperm ampulla, thereby ensuring maximum insemination. This hypothesis was tested in decorated crickets, *Gryllodes supplicans*, by comparing ampulla retention times of females guarded by their mates with those of unguarded females. There was no difference in ampulla attachment duration between the two groups, thus falsifying the 'ampulla-retention assurance' hypothesis. Two additional hypotheses related to the function of mate guarding were also tested: (1) mate guarding allows a male to remain in close proximity to his mate during the time it takes to produce a new spermatophore and (2) guarding functions to deter rivals from courting the recently mated female. The 'spermatophore renewal' hypothesis was rejected because the average inter-copulatory interval of males greatly exceeded the average guarding duration. The 'courtship reduction' hypothesis was supported by four lines of evidence: (1) guarded females were less likely to be courted by intruders than were females whose mates had been removed, (2) unguarded females mounted intruders significantly more often than guarded females, (3) the ampullae of unguarded females were more likely to be partially dislodged by the copulatory attempts of intruding males than were those of guarded females, and (4) guarded females were more likely to be maximally inseminated than were unguarded females.

In various insect species, males guard females after mating and such behaviour usually functions to deter the female from remating with other males (Thornhill & Alcock 1983). Guarding serves to increase a male's fitness by reducing the probability that his sperm will have to compete with the sperm of his rivals for the fertilization of a female's eggs (Parker 1970, 1984). Post-copulatory mate guarding occurs in crickets (Orthoptera: Gryllidae; Khalifa 1950; Alexander & Otte 1967), but its function remains unclear. This study was designed to determine the adaptive significance of post-copulatory mate guarding in the decorated cricket, *Gryllodes supplicans* (Orthoptera: Gryllidae), a species for which other aspects of copulatory behaviour have been examined in some detail (Sakaluk 1984, 1985).

In crickets, copulation is completed when the male transfers a spermatophore, which usually consists of a small sperm-containing ampulla that hangs outside the female's body after mating (Alexander & Otte 1967). The spermatophore is drained as sperm enter the female's genital tract through a narrow spermatophore tube inserted in the female's bursa copulatrix. In most species, the female eventually disposes of the spermatophore by consuming it (Loher & Rence 1978; Sakaluk & Cade 1980, 1983), and often does so before the spermatophore has been emptied of sperm (Sakaluk 1984, 1987; Simmons 1986). Male crickets initiate guarding behaviour immediately after copulation and attempt to remain in close proximity to their mates by employing a variety of tactics, including: (1) passively standing immediately adjacent to the female, (2) frequently antennating the female, (3) searching rapidly whenever the female wanders out of range of the male's antennae, (4) producing aggressive chirps upon any movement by the female or upon intrusion by another male and (5) physically attacking males that intrude (Khalifa 1950; Alexander & Otte 1967).

There are at least three hypotheses that could account for the post-copulatory guarding behaviour of male crickets. First, mate guarding may function to prevent the early removal of spermatophores by females, thus ensuring that females are maximally inseminated (Alexander 1961, 1962; Loher & Rence 1978; Zuk 1987). In support of this hypothesis, a correlation between guarding time and the duration of spermatophore attachment has

been shown for a variety of species (Loher & Rence 1978 and references; Graham 1982). Although such a correlation is consistent with the hypothesis, it does not directly demonstrate that male guarding controls the ampulla-removal behaviour of females. For example, ampulla removal might be entirely under female control, with females leaving their mates shortly before or immediately after consuming the sperm ampulla.

This 'ampulla-retention assurance' hypothesis also poses an apparent theoretical difficulty, at least as it applies to *G. supplicans*. In this species, the male provides the female with a courtship food gift, the spermatophylax, a specialized portion of the spermatophore that the female consumes after mating (Alexander & Otte 1967). This gift functions to keep the female preoccupied while sperm drain from the remaining portion of the spermatophore (i.e. the sperm ampulla) into her body (Sakaluk 1984, 1987). However, the provision of a spermatophylax does not rule out the possibility that guarding functions in a similar manner. Should the female discard the spermatophylax or consume it quickly (as often happens; Sakaluk 1984, 1987), it may be that mate guarding acts as a form of insurance, deterring a female that is no longer preoccupied with consuming the spermatophylax from prematurely removing the sperm ampulla.

A second hypothesis is that guarding allows a male to maintain close physical proximity to his mate during the time it takes to manufacture a new spermatophore, thus permitting repeated copulations with the same female (Khalifa 1950; Alexander & Meral 1967; Loher & Rence 1978). This 'spermatophore renewal' hypothesis assumes that multiple matings with the same female are adaptive. In support of this assumption, Sakaluk (1986) and Simmons (1987) have shown that the fertilization success of a male's sperm, relative to that of rivals' sperm, depends partly on their numerical representation in the female's spermatheca.

A third hypothesis is that mate guarding functions to deter other males from courting the female, thereby reducing the probability of the females' remating and the concomitant risk of sperm competition. Failure to prevent access of rivals to the female can be costly to a male in several other respects. (1) A recently mated female will often mount another courting male, and the thrusting actions involved in an attempted copulation may

dislodge the ampulla of the female's previous mate (Spann 1934; Loher & Rence 1978; Sakaluk 1987). (2) Even if the ampulla is not dislodged, a female often removes the ampulla of her previous mate after an unsuccessful mating with another male (personal observations). (3) A mated female that is left unprotected may have her ampulla stolen and consumed by a conspecific of either sex (Sakaluk 1987). Thus, the 'rival exclusion' hypothesis suggests that mate guarding may prevent premature removal of a male's ampulla, not through direct control of a female's behaviour, but rather through exclusion of competitors.

I conducted experiments to determine the function of post-copulatory mate guarding under two conditions: (1) in the presence of rival males and (2) in the absence of rival males. The three hypotheses and their attendant predictions under the two experimental conditions are summarized in Table I.

METHODS

Collection and Rearing Procedures

Experimental subjects were descendants (F_5) of approximately 60 adult *G. supplicans* collected at various locations in Tucson, Arizona, in May 1987. Captive crickets were housed in a glass terrarium and provisioned with Purina Cat Chow and water in vials plugged with cotton wicks. The effective surface area of the terrarium was increased by the addition of several egg cartons as a form of shelter. Eggs were obtained by allowing adult females to oviposit in 0·1-litre plastic weighing dishes filled with a mixture of equal amounts of moistened sand and vermiculite. Offspring were reared in plastic shoe boxes measuring $16·5 \times 30·5 \times 8·5$ cm, provisioned in the same manner as the adults, and held in environmental chambers maintained at $30 \pm 1°C$ on a 12:12 h light:dark cycle. Two holes, each 5 cm in diameter, were drilled in the cover of each cage and covered with metal screen to permit adequate ventilation. To ensure the production of robust adult stock, densities in rearing cages were maintained at low levels, ranging from five to 12 crickets per cage. Individuals of known age and mating status were obtained by isolating crickets by sex in separate cages immediately after the imaginal moult.

General Methods

All matings were staged in plastic shoe boxes during the dark portion of the photoperiod within

Table I. Hypotheses concerning the function of post-copulatory mate guarding in crickets and their attendant predictions

	Predictions	
Hypothesis	Male/female pairs no rivals present	Male/female pairs rivals present
(1) Ampulla-retention assurance	$a > b$	$a > b$ $e = f$ $g = h$
(2) Spermatophore-renewal	$c \geqslant d$	$c \geqslant d$
(3) Rival exclusion	$a = b$	$a > b$ $e < f$ $g < h$

a: Ampulla attachment times of guarded females.
b: Ampulla attachment times of unguarded females.
c: Guarding times of males.
d: Spermatophore replacement times of males.
e: Courtship attempts by rivals when guard present.
f: Courtship attempts by rivals when no guard present.
g: Remounting frequencies of guarded females.
h: Remounting frequencies of unguarded females.

4–10 h of 'lights off', the period during which decorated crickets are most active (Sakaluk 1987). Observations were made under the illumination provided by a 25-W incandescent red light. No food or water was provided during experimental trials (unless otherwise stated), and cages were washed with detergent and water between trials. Even when confined with males, female *G. supplicans* cannot be forced to copulate, and preliminary observations showed that mating cages were sufficiently large to allow females to elude guarding males should they choose to do so. Thus, the experimental protocol used here can be considered a reasonable approximation of sexual interactions that take place in the field once pairs have been established. Data from all experiments were analysed using the procedures of the Statistical Analysis System for personal computers (SAS Institute 1988). All values given are mean ± SE.

Experiment 1: Ampulla-retention Assurance Hypothesis

To test the ampulla-retention assurance hypothesis, three experimental groups, each consisting of a number of male–female dyads, were established. Group 1 consisted of 15 undisturbed pairs in which the male was permitted to guard the female after mating. Group 2 consisted of 20 pairs in which the male was removed from the mating cage immediately after mating. Group 3 consisted of 15 pairs in which the male was removed immediately after mating, but then immediately placed back with the female. For each pair that mated, I recorded the ampulla attachment time of the female and observations of post-copulatory interactions between males and females.

The hypothesis predicts that females with a guarding male (group 1) should retain the spermatophore for significantly longer periods than females without a guarding male (group 2). Group 3 was a control for any disturbance caused to females in the second group by the act of removing the male. If the disturbance per se has no effect on spermatophore retention, then the spermatophore attachment times of group 3 females should not be significantly different from those of group 1 females. This is an effective control because males, even after being physically handled, resume guarding within seconds of being placed back with the female (personal observation).

With the exception of 10 females in group 2, experimental females were virgins and between 10 and 18 days old (adults). To determine whether previous mating experience had any effect on the ampulla retention time of females, 10 of the unguarded females of group 2 were housed with males prior to experimental trials and presumably

were non-virgin at the time of testing. Males used in experimental trials had previous mating experience and were between 4 and 18 days old of adult age. Males were isolated from females 24 h prior to trials to ensure their sexual readiness.

Experiment 2: Spermatophore Renewal Hypothesis

To test the spermatophore renewal hypothesis, I recorded the guarding durations of males for nine of the male–female dyads in group 1 (above) and five additional undisturbed pairs (total $N = 14$). The average guarding duration was compared with the average inter-copulatory interval of 20 other males allowed continuous access to sexually receptive females. To determine this latter value, I used non-virgin males and females of unknown age; they were held separately for 3–5 days prior to observations to ensure their sexual readiness. Each male was placed in a mating cage with two females, along with food and water. Observations began 4 h after 'lights off'. After an initial mating, the mated female was removed and replaced with a fresh female and observations continued until a second mating occurred or until 6 h had elapsed. The times at which first and second matings occurred were recorded for each male. The hypothesis predicts that the average guarding duration of males should be equal to or exceed the average inter-copulatory interval, assuming that male inter-copulatory interval is a reliable estimate of the time it takes a male to produce a new spermatophore. The assumption is supported by the observation that males can store only one spermatophore at a time in the spermatophoric pouch and, once transferred, another spermatophore must be manufactured de novo (e.g. Loher & Rence 1978).

Experiment 3: Rival Exclusion Hypothesis

To test the rival exclusion hypothesis, I established two experimental groups, each consisting of 20 triads. Each triad consisted of two males and one female. In group 1 triads, the male that succeeded in mating with the female was permitted to guard her against the subsequent copulatory attempts of the unmated male (the 'intruder'). In group 2 triads, the male that succeeded in mating with the female was removed immediately after the mating. For each triad, I recorded the duration of ampulla attachment of the female and the frequency with which the mated female mounted the intruder while the

previous ampulla was still attached. I also recorded my observations of the interactions between males, and those between each of the males and the female. The hypothesis, as outlined earlier, makes three predictions: (1) ampulla retention times of females with guards present to expel intruders should be significantly longer than those of unguarded females, (2) courtship attempts of rival males should be reduced when guards are present, and (3) remounting frequencies of guarded females should be lower than those of unguarded females.

RESULTS

Experiment 1: Ampulla-retention Assurance Hypothesis

Considering only those females for which the male was removed immediately after copulation (group 2), there was no significant difference in the mean ampulla attachment duration of previously virgin (33.83 ± 7.27 min) and non-virgin females (31.06 ± 5.83 min; Student's t-test, $t = 0.30$, $P > 0.05$). Because a female's prior mating status apparently had no effect on her proclivity to remove the ampulla, data obtained from virgin and non-virgin females of group 2 were combined in subsequent analyses.

Mean ampulla retention durations of guarded females (36.96 ± 4.40 min), unguarded females (32.45 ± 4.55 min), and control females (36.69 ± 4.89 min) were not significantly different (one-way ANOVA, $F = 0.32$, $df = 49$, $P > 0.05$). Thus, the hypothesis that guarding behaviour prevents premature ampulla removal must be rejected.

I commonly observed a number of stereotypic behavioural acts in post-copulatory interactions of undisturbed pairs (group 1). When guarding, the male typically stood motionless within 1 cm of the female, facing away and with his cerci (a pair of filamentous appendages extending from the terminal end of the abdomen) pointed directly toward the female. Occasionally, the male would rapidly vibrate his antennae, but this occurred without any obvious external stimulus. Females, for the most part, remained relatively quiescent during the majority of the guarding period. Any movement on the part of the female usually resulted in some reaction by the male. Most commonly, he would turn, antennate the female and, if she remained still, the male would resume the basic guarding position. Less commonly, the male would remain in the typical guarding position, but engage in a short series of
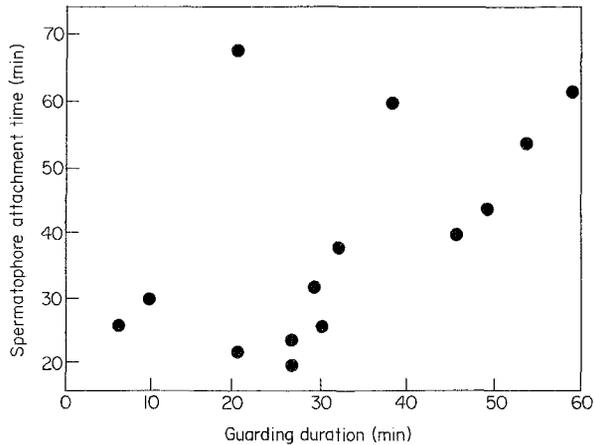
Figure 1. The correlation between the duration of male guarding and the duration of ampulla attachment. Significant at $P < 0.05$ (Pearson $r = 0.54$, $N = 14$).

rapid 'push-ups' in which he briefly raised his body by extending his legs.

At various times during the guarding period, females appeared to become 'restless', as evidenced by rapid movement of the female's antennae, attempts to remove the externally attached ampulla, or movement away from the guarding male. Such behaviour became most evident shortly before or after the female had fully consumed the spermatophylax. Whenever the female walked away from the male, he usually followed her, remaining in physical contact with her through the use of his antennae. Females either became quiescent following this initial movement or only momentarily ceased walking before moving away again; such behaviour often resulted in a series of jerky 'stop-and-starts' by the female and her mate. Whenever the female wandered out of range of the male's antennae, the male would often make rapid, apparently random, searching movements in his immediate area until regaining contact with the female. I considered guarding to have ceased whenever the female moved away from the male and he made no attempt to follow her or resume guarding upon re-contact, or whenever the male walked away from the female without paying further attention to her.

I observed only one behavioural act that could be construed as an attempt by the male to prevent premature removal of the ampulla, and it was witnessed in only one of the 15 interactions described here and on two previous occasions. Such behaviour occurred when the female bent the tip of her abdomen towards her mouthparts to remove the ampulla; in an apparent response to that movement, the guarding male turned to face the female and butted her with his head. This act caused the female to withdraw her abdomen without removing the ampulla.

Experiment 2: Spermatophore Renewal Hypothesis

All males allowed continuous access to females mated and 15 of the 20 remated within the 6-h observation period. The mean inter-copulatory interval of twice-mated males (251.54 ± 12.23 min, $N = 15$) was approximately eight times longer than the mean guarding duration of males (31.71 ± 4.22 min, $N = 14$), and this difference was highly significant (*t*-test for unequal variances, $t = 16.87$, $P < 0.0001$). I therefore reject the hypothesis that guarding enables a male to remain in close proximity to the female until he is able to remate with her. There was a significantly positive correlation between the guarding duration of the male and the ampulla retention time of the female (Pearson $r = 0.54$, $P < 0.05$; Fig. 1). In five of the 14 matings, males continued to guard the female after she had removed the ampulla.

Experiment 3: Rival Exclusion Hypothesis

Guarded females retained their ampullae 6 min longer, on average, than females without a guarding male (43.93 ± 3.83 min versus 37.78 ± 3.60 min), but this difference was not statistically significant (*t*-test, $t = 1.17$, $P > 0.05$). However, this comparison ignores those instances in which the ampulla was

partially dislodged through the copulatory efforts of rival males. Often when mated females mounted males, the spermatophore tube was partially pulled out of the female's bursa copulatrix as a consequence of force exerted on the ampulla through the thrusting actions of the male. The ampulla was partially dislodged significantly more often when no guard was present (10 interactions) than when a guard was present (two interactions; Fisher's exact test, one-tailed, $P = 0.007$). Since partial dislodgement of the ampulla may interrupt the transfer of sperm from the ampulla to the female, I re-calculated mean durations of ampulla attachment using time of ampulla removal or partial dislodgement to mark the end of ampulla retention. When adjusted in this manner, the mean ampulla retention duration of guarded females (42.24 ± 4.42 min) was significantly greater than that of unguarded females (19.50 ± 3.24 min; t-test, $t = 38.0$, $P < 0.0002$).

I also compared the proportion of males in each group that transferred a complete ejaculate, assuming that a minimum spermatophore retention time of 50 min is required for the complete evacuation of the ampulla (see Sakaluk 1984 for the rate of sperm transfer in *G. supplicans*). Nine of 20 females with a guard present retained the ampulla for a minimum of 50 min, whereas only four of 20 females without a guard present retained the spermatophore for this duration; this difference was, however, not quite significant (Fisher's exact test, one-tailed, $P = 0.088$). In two instances, the ampulla was wholly dislodged due to the thrusting actions of the intruding male, and in both of these cases, the intruding male transferred a spermatophore immediately thereafter. Theft of the spermatophore by the intruding male also occurred on two occasions, and in each case, the intruding male detached the spermatophylax from the ampulla (which remained attached to the female), and consumed it.

I observed little overt aggression between guarding males and intruders. Instead, the guarding male typically adjusted his position relative to the female such that his body was always between the female and the intruder. As a consequence of this spatial arrangement, the intruding male frequently misdirected his courtship behaviour towards the guarding male, and was apparently unable to distinguish the sex of the individual he courted while facing away from the mated pair (sexual recognition requires contact of the female's body by the

male's antennae: Rence & Loher 1977; Hardy & Shaw 1983). Aggressive behaviour was observed on only two occasions, and in each case involved a short burst of aggressive calling by both males who also kicked at each other with their hind legs.

Unguarded females mounted intruders significantly more often than guarded females (3.15 ± 0.99 mounts versus 1.05 ± 0.39 mounts; Kruskal–Wallis, one-tailed, $P < 0.025$). The intruder courted the mated female at least once in 19 of 20 interactions when no guard was present, whereas the intruder courted the female in only 14 of 20 interactions when a guard was present; this difference was also statistically significant (Fisher's exact test, one-tailed, $P = 0.046$).

DISCUSSION

The results of this study show that post-copulatory mate guarding by male decorated crickets does not prevent the female from prematurely removing the sperm ampulla. None the less, a positive correlation between male guarding duration and the ampulla retention time of the female was observed. Such evidence has, in the past, been used to support the ampulla-retention assurance hypothesis (reviewed in Loher & Dambach 1989). In contrast to this interpretation, I suggest that the correlation between guarding duration and ampulla retention time may arise incidentally as a result of the timing of the female's departure from the male. In support of this contention, female *G. supplicans* characteristically became 'restless' and began actively trying to elude the male shortly before removing the ampulla, and it is the temporal coincidence of these events that may have caused the observed correlations. Further support for this hypothesis is provided by Evans' (1988) comparative study of three Australian gryllids. She observed that female *Teleogryllus commodus* and *Balamara gidya* retained their ampullae for significantly longer durations when they remained with males after copulation than when they left males shortly after copulation, but interpreted this result as favouring the ampulla-retention assurance hypothesis.

In comparison with the correlational evidence, direct tests of the ampulla-retention assurance hypothesis have been few, and the results of these studies have been mixed. In support of the hypothesis, Loher & Rence (1978) found that the ampulla-retention times of female *T. commodus* whose mates

had been removed were significantly shorter than those of females whose mates were permitted to guard them after mating. In contradiction of the hypothesis, Khalifa (1950) and Sakaluk & Cade (1980) found that the ampulla-retention times of female *Acheta domesticus* that were isolated from their mates did not differ significantly from those of females kept with guarding males. Simmons (1986) also found no obvious effect of guarding on ampulla-retention duration in *Gryllus bimaculatus*, and suggested that Loher & Rence's (1978) results may have been an artefact of the confinement of mated pairs to small observation cells, which allow females little opportunity to elude males. Loher & Dambach (1989) responded to this criticism by suggesting that observations of guarding behaviour in small mating cells are closer to the natural situation than are those taken from large open arenas (as in Simmons 1986), because mating in *T. commodus* usually occurs in the confines of the male's burrow where the male has a greater opportunity to sequester the female. Neither criticism seems particularly germane to the present study, since male *G. supplicans* in natural and semi-natural environments routinely establish calling sites in both burrows and open terrain (Sakaluk 1987 and personal observation).

The results of the present study also do not support the hypothesis that guarding enables a male *G. supplicans* to remain in close proximity to the female until he is able to mate with her again. The average inter-copulatory interval of males allowed continuous access to females was approximately eight times longer than the average guarding duration; this suggests that the guarding period is of insufficient duration to permit a male to produce a new spermatophore. By way of contrast, the average spermatophore replacement time of male *T. commodus* is comparable to their average guarding duration. Even in this species, however, the male does not resume courtship of a previous mate until 35–40 min after guarding has ceased (Loher & Rence 1978; Loher & Dambach 1989).

The rival exclusion hypothesis appears to best explain the results obtained for *G. supplicans*, although in one respect, the evidence is equivocal. Guarded females tended to retain their spermatophores longer than unguarded females, but this difference was not statistically significant. However, the ampullae of unguarded females were more likely to be partially dislodged by the copulatory attempts of intruding males than were those of guarded females. When ampulla attachment durations were compared on the basis of complete retention of the ampulla, guarded females retained their ampullae significantly longer than unguarded females. Morever, unguarded females were courted more often by intruders and mounted intruders significantly more often than guarded females. Males also were more likely to transfer a full ejaculate when permitted to guard against intruders, than when they were removed after mating. These results suggest that by deflecting the courtship attempts of rival males, guarding males reduce the remounting frequencies of their mates and also reduce the concomitant risks of ampulla displacement.

Acceptance of the rival exclusion hypothesis as a tentative explanation for the origin of male guarding behaviour requires that: (1) mated pairs are confronted at least occasionally by rival males and that (2) even a short delay in mounting of rival males by mated females results in increased fitness to guarding males. With respect to the first requirement, studies in natural and semi-natural habitats have shown that nearest-neighbour distances of calling male *G. supplicans* are uncommonly small and that two or more males may share the same burrow (Sakaluk 1987). Thus, there is ample opportunity for males to court the recent mates of rivals. With respect to the second requirement, there are at least two ways in which a reduction in the frequency of remounting by females might benefit a guarding male. First, guarded females are more likely to permit the complete evacuation of the ampulla and less likely to have their ampullae wholly or partially dislodged through the copulatory efforts of intruding males. Increased ampulla attachment durations result in a greater transfer of sperm (Sakaluk 1984), which in turn increase the probability that a male will fertilize at least some of a female's eggs (Sakaluk 1986; Simmons 1987). Second, a delay in remounting by the female would allow greater time for any anti-aphrodisiacs transferred in the ejaculate to take effect (see Gilbert 1976). Although no such substance has been identified for any cricket species, Cade (1979) showed that the phonotactic response of female *Gryllus integer* was significantly depressed after only 1 day of confinement with males.

Although the data for *G. supplicans* tend to support the rival exclusion hypothesis, an examination of the comparative evidence suggests that guarding behaviour may serve different functions in different species. For example, mate guarding may

Table II. Interspecific variation in the form and intensity of post-copulatory mate-guarding behaviour in crickets

Species	Mate guarding	Guarding posture	Guarding time (min)	Stereotypic guarding behaviour			Source
				Push-ups	Head butting	Aggressive stridulation	
Gryllinae							
Gryllodes supplicans	+	Cerci*	32	+	+	Rarely	Present study
Teleogryllus commodus	+	Antennae†	83	−	+	+	Loher & Rence 1978
Acheta domesticus	+	Antennae	55	+	−	+	Fleishli & Sakaluk, unpublished data
Gryllus assimilis	−	−	−	−	−	−	Spann 1934
Nemobiinae							
Nemobius sylvestris	+	Antennae	11 and 19‡	−	−	+	Campan & Demai 1983
Bobilla victoriae	+	?	Conditional§	?	?	+§	Evans 1988
Hygronemobius alleni	−	−	−	−	−	−	Mays 1971
Trigonidiinae							
Balamar gidya	+	?	11	?	?	?	Evans 1988

+: the behaviour is performed; −: behaviour is not performed; ?: insufficient data.
*Male guards with his cerci directed toward the female.
†Male guards with his antennae directed toward or across the female's body.
‡Male transfers two spermatophores in a mating sequence and guards after the transfer of each one.
§Male does not guard immediately after mating but guards if female attempts to leave. Female consumes spermatophore 2 min after mating during which time the male produces a post-copulatory calling song.

function to prevent premature ampulla removal in some species (e.g. *T. commodus*) and serve to exclude competitors in others (e.g. *G. bimaculatus, G. supplicans*). The possibility of multiple functions to post-copulatory guarding is supported by various interspecific differences in the form and intensity of male guarding behaviour that exist throughout the gryllids (Table II).

Since little attention has been paid to the various behavioural acts that occur during the guarding period, preliminary hypotheses concerning their function seems warranted. *Gryllodes supplicans* is the only species in which the male guards facing away and with his cerci directed toward the female. I suggest that the male adopts this posture because it allows him to detect any movement by his mate while, at the same time, enables him to determine the sex of an approaching conspecific. The cerci of crickets are covered by a dense coat of long filiform hairs that are acutely sensitive to air currents (Dambach & Rausche 1985; Kämper & Dambach 1985); presumably, such currents are generated by movement of the female. In apparent response to female movement, the male either turns to antennate her or remains in the guarding position and performs a 'push-up'. Antennation probably confirms the female's presence. 'Push-ups' may serve to communicate to the female, via the generation of air currents, the continued attentiveness of the male. 'Head butts', when they occur, may function to momentarily deter a female who is in the act of removing the ampulla (Loher & Dambach 1989).

Mating behaviour is often viewed in the context of a conflict of interests between the sexes, one in which males are preordained to win because of the greater sexual selection operating on that sex (Parker 1979). However, the present study suggests that female *G. supplicans* determine the degree to which they are inseminated by their mates and therefore control, to some extent, male fitness. Future studies will examine the extent to which females employ ampulla removal as a mechanism for expressing mating preferences.

ACKNOWLEDGMENTS

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