

Post-copulatory mate guarding delays promiscuous mating by female decorated crickets

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Post-copulatory mate guarding by male insects often functions to deter females from mating with other males (Alcock 1994). In most cricket species, a male guards his mate by standing motionless next to her, usually draping his antennae over her dorsum, and producing violent shaking motions upon any attempt by the female to move away or upon disturbance of the pair by an intruding male (reviewed in Loher & Damabach 1989). The adaptive significance of these patterns of guarding behaviour has proven difficult to establish and may differ among cricket species (Sakaluk 1991).

It is widely held that mate guarding by male crickets functions to deter the female from removing the externally attached spermatophore before it is emptied of sperm (e.g. Alexander 1961; Loher & Dambach 1989; Simmons 1991). Sakaluk (1991) tested this hypothesis in decorated crickets, *Grylodes sigillatus* (Orthoptera: Gryllidae), by comparing the length of time that guarded and unguarded females retained the sperm-containing portion of the spermatophore (sperm ampulla). There was no significant difference between treatments, refuting the spermatophore-retention assurance hypothesis. A second experiment provided support for an alternative hypothesis, namely, that guarding functions to exclude intruding males from the vicinity of the mated female, thereby preventing her from mounting rivals (Simmons 1986; Sakaluk 1991). To test this hypothesis, Sakaluk (1991) established triads consisting of two males and one female in small observation arenas. In half of the replicates, all three individuals were left in the arena after mating occurred, with the mated male designated as the 'guard' and the unmated male the 'intruder'. In the remaining replicates, the guard

was removed from the arena immediately after mating while the intruder remained with the female. In accordance with the rival exclusion hypothesis, guarded females were courted by and mounted intruders less frequently, and were less likely to have their spermatophores dislodged by intruders.

Although Sakaluk's (1991) study permits rejection of the spermatophore retention hypothesis, his test of the rival exclusion hypothesis was flawed in at least three respects.

(1) Intra-sexual competition potentially confounds this test of mate guarding effectiveness because the mechanisms involved in intra-sexual competition may be similar to those involved in mate guarding. If true, a male's ability to secure a mating would not be independent of his ability to guard effectively.

(2) Males successful at mating may have been preferred over their rivals. Perceived guarding ability is therefore confounded with female mate choice, because females may have been reluctant to mount undesirable (rival) males.

(3) Cricket density differed between the two treatments owing to the removal of the mated male in one treatment. If density influences the encounter rate of intruders and mated females then the probability of the intruder being mounted by the female may have also been affected.

These considerations call into question Sakaluk's (1991) test of the rival exclusion hypothesis. We present the results of a more rigorous test of the rival exclusion hypothesis that avoids the potentially confounding effects of the previous investigation. Here male status (guard versus intruder) was assigned independently of intra-sexual interactions or female choice, and female receptivity and cricket density were held constant across treatments.

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Seven days after their imaginal moult, we removed virgin male and female *G. sigillatus* from the same stock colony used by Sakaluk (1991) and established two treatments, guard⁺ and guard⁻, respectively (described below). Prior to the start of the trials, we established a number of male-female dyads in small observation arenas (shoe boxes). Guard⁺ dyads were each composed of a sexually mature male and female, while guard⁻ dyads were composed of an immature, late instar male nymph and sexually mature female. In guard⁺ dyads, once copulation had occurred and the male had begun guarding the female, we immediately replaced her with another virgin female, presumed to be sexually receptive. Because males apparently cannot distinguish between females with whom they have mated and those with whom they have not (Sakaluk 1991), guard⁺ males resumed guarding the replacement females. Immediately after a guard⁺ male re-established guarding behaviour, we introduced a sexually mature male intruder to the arena, marking the beginning of the trial. Simultaneously, we initiated a companion guard⁻ trial by introducing a sexually mature male intruder to the arena of a guard⁻ dyad. Trials were observed under dim red light 2-6 h into the dark phase of a 12:12 h light:dark cycle and were terminated after 60 min. For trials in both treatments we recorded (1) the time at which the intruder was first mounted, (2) the number of times the intruder was mounted, and (3) the time at which a mating between the female and intruder occurred (i.e. a mount resulting in spermatophore transfer). We completed 19 guard⁺ trials and 20 guard⁻ trials. One guard⁺ trial was aborted because the initial male failed to court the female. In all other trials each adult male exhibited courtship behaviour. All initial males in guard⁺ trials exhibited post-copulatory guarding of their replacement females.

The rival exclusion hypothesis predicts that male intruders should take significantly longer to secure copulations with guarded females than with unguarded females. We employed failure time analysis (Pyke & Thompson 1986) to compare the mating success of intruder males in the guard⁺ and guard⁻ trials because intruders were not mounted in three guard⁺ trials, hence the data were right-censored. Copulations between guarded females and male intruders occurred significantly later than those involving unguarded females and intruders (log-rank test, $\chi^2=8.22$,

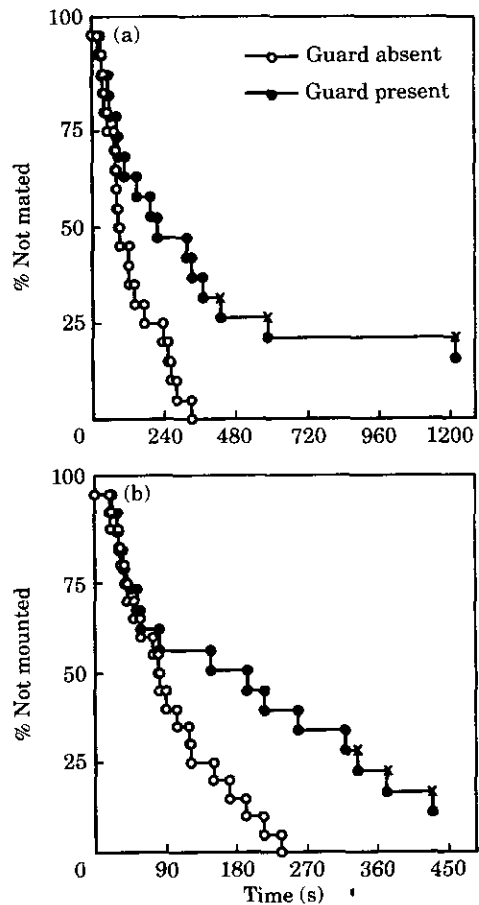


Figure 1. Mating success of male intruders in the presence and absence of guarding male *G. sigillatus*. Percentage of intruders that failed to (a) mate and (b) mount as a function of time. Points marked with \times are right-censored.

$P=0.0041$; Fig. 1a). These data support the rival exclusion hypothesis, namely, that post-copulatory mate guarding in *G. sigillatus* reduces promiscuous mating by females. Guarding males succeeded in thwarting their rivals even though guarded females were virgins and presumably of high sexual motivation. Under normal circumstances, guarding is likely to delay female re-mating even further owing to the decrease in sexual receptivity of females after mating (Loher & Dambach 1989). Because crickets are continuous egg layers and fertilization is based primarily on the numerical representation of competing males' sperm, even modest delays in female

re-mating should yield significant fitness benefits to guarding males (Sakaluk 1991).

Our experimental design also allows us to distinguish between two possible mechanisms by which guarding males exclude rivals.

(1) If guards physically deter intruders by placing themselves between intruders and the female, producing aggressive chirps, or physically attacking, then guarded females should have increased time to mount intruders compared to unguarded females.

(2) If guards actively disrupt copulations involving their mates and intruders, then guarded females should experience more failed mounts of intruders (mounts not leading to spermatophore transfer) than unguarded females.

Our results reveal that guards hinder male intruders from courting females, as indicated by the longer time to first mount of intruders in the guard⁺ treatments (log-rank test, $\chi^2=6.56$, $P=0.0104$; Fig. 1b). There was no difference in the mean number of failed mounts of intruders in the guard⁺ and guard⁻ treatments (1.4 and 2.0, respectively; $F_{1,37}=0.88$, $P=0.3532$), suggesting that once a female has mounted an intruder the guarding male has no means of successfully disrupting the pair. As observed by Sakaluk (1991), guards placed themselves between the intruder and the female, and were often courted by intruders (13 of 19 trials). Guarding males apparently engaged in a crude form of female mimicry, hampering the ability of intruders to induce females to mount (Fig. 1b; see also Field & Keller 1993).

Successful competition between males for access to females is likely to be related to some trait not directly considered in this study (e.g. male size; Dixon & Cade 1986). Under our experimental design, such a trait would have been randomly distributed among males in the two treatments and hence, about half of the guard⁺ males would have been subordinate to male intruders. Such a relationship is supported by the trajectories of the curves in Fig. 1. Within about 2 min of being introduced, approximately 30% of the male intruders had secured a mating. After 2 min, however, the trajectories of the two

treatments diverged rapidly; all of the intruders in the guard⁻ treatment mated within 5 min, whereas even after 20 min, about 20% of intruders in the guard⁺ treatment still had not mated. These results suggest that post-copulatory mate guarding is likely to be effective only when the guarding male is of higher intrinsic competitiveness relative to an intruder. Hence, post-copulatory mate guarding may actually amplify sexual selection of the same traits that are important in securing access to receptive females.

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