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Prolonged mate guarding and sperm competition in the weevil *Diaprepes abbreviatus* (L.)

Ally R. Harari,[a] Peter J. Landolt,[a] Charles W. O'Brien,[b] and H. Jane Brockmann[c]
[a]USDA-ARS, PO Box 14565, Gainesville, FL 32604, USA, [b]Center for Biological Control, Florida A & M University, Tallahassee, FL 32307-4100, USA, and [c]Department of Zoology, University of Florida, Gainesville, FL 32611-8525, USA

The hypothesis that prolonged copulatory mate guarding coexists with last male sperm precedence was tested for the sugarcane rootstalk borer weevil, *Diaprepes abbreviatus* (L.) (Coleoptera: Curculionidae). Male *D. abbreviatus* showed a long copulatory guarding. Both males and females were less likely to remate when prolonged guarding occurred compared with terminating copulation early. Guarding was generally terminated by the struggling behavior of the female. Mating experiments using normal and sterile (X-ray irradiated) males revealed a similar value of last-male sperm precedence for both irradiated and normal males. The P_2 values of normal and sterile males were similar when all oviposited eggs were counted over 30 days. These data made it possible to calculate the expected gain to a male from prolonged guarding compared with leaving a female early and seeking out an additional mate. We show that guarding has the higher fitness. Eggs were deposited in clutches in which normal fertilized eggs were grouped together and were attached to a group of sterile eggs. This, together with identifying the form of the cul-de-sac type spermatheca, allowed us to suggest a unique repositioning process, which has not been described elsewhere, as the likely mechanism by which last-male sperm precedence was achieved. *Key words:* copulation guarding, cul-de-sac spermathecae, sperm precedence. *[Behav Ecol 14:89–96 (2003)]*

Prolonged copulatory guarding is a well-described phenomenon in insects and is usually explained as a male adaptation to avoid sperm competition (Simmons, 2000; Thornhill and Alcock, 1983). Mate-guarding involves tradeoffs for males because it consumes time and energy that could be used for finding and mating additional females. It evolves when a male that remains with a single female has greater fitness than a male that seeks additional mating opportunities. Under this explanation, copulatory guarding is expected only when last-male sperm precedence occurs (McLain, 1989; Parker, 1979; Telford and Dangerfield, 1990): if the male stops guarding and the female remates, then most of the eggs she lays will be fertilized by the final male to mate with her.

An alternative hypothesis exists: females may benefit from prolonged male mate-guarding. This can occur through one of two mechanisms. (1) If female fitness is increased by mating with larger males, if mate guarding and male-male competition results in larger males guarding longer than smaller males do, and if the last male to mate fertilizes most of the female's eggs, then mate guarding can increase female reproductive success through direct or indirect benefits (Harari et al., 1999; Simmons et al., 1996). (2) If prolonged copulatory guarding reduces predation, improves female survivorship (Gwynne, 1989; Sivinski, 1983), enhances foraging efficiency (Wilcox, 1984), or saves females time and energy by preventing harassment by searching males (Rowe, 1992; Waage, 1979a), then female fitness is increased when males guard. These explanations suggest that females may play an important role in determining the occurrence and duration of copulatory guarding behavior and that mate guarding cannot be thought of simply as a male adaptation for sperm competition (Jablonski and Vepsäläinen, 1995; Simmons, 1987).

Experimental studies of sperm precedence in insects have revealed that some degree of sperm competition usually occurs after successive inseminations. In most cases, the ejaculate of the last male to mate achieves more than 50% of the fertilizations (Parker, 1984; Simmons, 2000). Several mechanisms for last-male sperm precedence in insects have been suggested: (1) replacement involves removing of rival sperm before insemination with special structures of the penis (Gage, 1992; Siva-Jothy, 1987; Waage, 1979b) or flushing-out sperm, which occurs when new sperm fills up the storage organ and the previous sperm is pushed out (Otronen, 1990); (2) dilution is quantitative competition in which the second male to mate deposits more sperm than was stored from previous matings (Gage, 1991; Newport and Gromko, 1984; Simmons, 1987); (3) destruction occurs when the effective number of previously stored sperm is reduced by the second male through chemical or physical means (Gack and Peschke, 1994; Harshman and Prout, 1994); and (4) repositioning is spatial competition in which the second male to mate moves the sperm within the female's storage organ so that his sperm are more likely to fertilize the eggs (Eady, 1994a,b; Siva-Jothy, 1987). These are male-centered explanations. Females also play an important role in determining the use of sperm (Birkhead and Parker, 1997; Eberhard, 1996).

Female behavior, morphology, and physiology can also influence the process of transferring or storing sperm, the competitive ability of the ejaculates from different males, and, of course, the probability of remating (Birkhead et al., 1993; Eberhard, 1996).

Preliminary observations revealed that males of the West Indian sugarcane rootstalk borer, *Diaprepes abbreviatus* (L.) (Coleoptera: Curculionidae) exhibit intense copulatory

Address correspondence to A.R. Harari, who is now at Department of Entomology, The Volcani Center, Bet Dagan, 50250, Israel. E-mail: ally@int.gov.il. P.J. Landolt is now at the USDA-ARS, Wapato, WA 98951, USA.

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guarding: they maintain genital contact long after insemination has occurred. Rival males are attracted to mated pairs (Harari and Landolt, 1997; Harari et al., 2000), and takeovers are common (Harari et al., 1999). Such behavior results in the prediction that last-male sperm precedence should occur in this species. Last-male sperm precedence has been demonstrated in other curculionids such as the plum curculio, *Conotrachelus nenuphar* (Huettel et al., 1976), and the boll weevil, *Anthonomus grandis* (Bartlett et al., 1968), but not in *D. abbreviatus*. The goals of this study are (1) to evaluate the prediction that prolonged copulatory mate-guarding behavior of *D. abbreviatus* is associated with sperm competition and last-male sperm precedence; (2) to examine the hypothesis that male guarding conveys higher reproductive success for males than does searching for additional females with which to mate; (3) to examine whether mate guarding is likely to increase female reproductive success; and (4) to describe the likely mechanism by which sperm precedence is achieved. (5) In addition, because of the unusual way in which female *D. abbreviatus* lay their eggs, we also describe the pattern of differential sperm use by the female after mating with two males.

METHODS

Adult male and female *D. abbreviatus*

Adult *D. abbreviatus* were collected from ornamental trees near Apopka, Orange County, Florida, on nine different occasions during the spring and summer of 1995–1996. Virgin laboratory-reared females and males were acquired from USDA–ARS, Orlando, Florida, USA. All weevils were sexed in the laboratory (Harari and Landolt, 1997). Up to 50 weevils of each sex were maintained in separate Plexiglas frame cages ($30 \times 30 \times 30$ cm) with five sides of 1-mm mesh screening and a Plexiglas bottom. They were fed green beans and kept on the local day length for that time of year (May–October). A double parafilm sheet (3 cm wide $\times$ 10 cm long) was attached with adhesive tape to the inside wall of the females' cages to provide oviposition substrate. These strips were replaced daily. The Plexiglas cages were kept in different field cages ($3 \times 3 \times 3$ m) located 50 m apart, outside of USDA-ARS in Gainesville, Florida, USA, and exposed to outdoor conditions. Field-collected weevils were held for at least 10 days before the experiments to ensure female sexual receptivity. During experiments, adult male and female weevils were placed together in Plexiglas cages and kept under 12 : 12 h light : dark schedule (dawn at 0700 h).

Copulatory guarding

In *D. abbreviatus* the male remains on the female's back in copulatory position with the aedegus continually inserted for more than 16 h. Preliminary experiments demonstrated that females who mate for only 60 min oviposit as many eggs as do females that mate and were guarded all day. The outcome of male-male competition depends, in large part, on the relative size of the two males, with larger males displacing smaller guarding males more easily (Harari et al., 1999, 2000).

Guarding is generally terminated by the struggling behavior of the female. However, when males terminate guarding,

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