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PATTERNS AND CONSEQUENCES OF MATING BEHAVIOR OF THE ROOT WEEVIL *DIAPREPES ABBREVIATUS* (COLEOPTERA: CURCULIONIDAE)

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ABSTRACT

The tropical root weevil, *Diaprepes abbreviatus* (L.), is a major pest of many plants of economic importance, including citrus and ornamentals. It was accidentally introduced from the Caribbean into Florida in the 1960s and its range within the United States now includes Texas and California. No safe and effective control method is available for this species. Studies of the reproductive behavior of field populations may aid the development of effective control strategies and inform laboratory experimental design. We examined mating patterns of individually-marked *D. abbreviatus* in a plant nursery in Florida over 5 d. Matings occurred throughout the day but tended to peak during the middle of the day. Mating duration ranged from less than 3 h to over 9 h. Most males and females mated repeatedly, sometimes with the same partner multiple times. Both same-sex and extra-pair mountings occurred at low frequencies. In a follow-up study conducted in captivity, we found no short-term direct benefits of multiple mating to females but female fertility decreased dramatically by 2 weeks after mating if females were not allowed to re-mate. Thus, female *D. abbreviatus* may re-mate, in part, to replenish sperm stores. Our results suggest that the sterile insect technique would not be effective but support previous conclusions that pheromones may be effective attractants in this species because both females and males mate multiple times in the field.

Key Words: reproduction, beetle, mating frequency, fecundity, fertility

RESUMEN

El picudo *Diaprepes abbreviatus* (L.) es una plaga de plantas de importancia económica tales como los cítricos y plantas ornamentales. Fue introducido por primera vez del Caribe a la Florida en los años sesenta y su rango dentro de los Estados Unidos se ha extendido hasta Texas y California. Por el momento no se ha desarrollado un método de control seguro y efectivo en contra de la especie. Estudiamos el comportamiento reproductivo de poblaciones silvestres para promover el desarrollo de estrategias de control e informar diseños experimentales de bioensayos. Nosotros examinamos patrones de apareamiento de individuos marcados de *D. abbreviatus* en un invernadero comercial en el sur de Florida durante 5 días. Observamos apareamiento durante todo el día con una tendencia a aumentar al mediodía. La duración del apareamiento vario desde <3 hasta >9 horas. La mayoría de los machos y hembras se aparearon repetidamente, a veces con el mismo individuo. Acoplamientos entre individuos del mismo sexo o apareamientos entre >2 individuos ocurrieron a frecuencias bajas. En un estudio de seguimiento conducido en cautiverio, no encontramos beneficio para las hembras a corto plazo de los apareamientos múltiples. La fertilidad disminuyó dramáticamente dos semanas después del apareamiento cuando se negó la posibilidad de re-aparearse. Por lo tanto, hembras de *D. abbreviatus* podrían re-aparearse, en parte, para renovar su reserva de esperma. Nuestros resultados sugieren que la técnica de insectos estériles no seria efectiva en el caso de *D. abbreviatus*, pero apoyan conclusiones previas de que las feromonas pueden usarse como atrayentes en esta especie ya que tanto hembras como machos se aparean múltiples veces en el campo.

Translation provided by the authors.

Diaprepes abbreviatus (L.) is a tropical root weevil thought to be native to Puerto Rico and the Lesser Antilles and is currently found over much of the Caribbean, and in Florida, California, and Texas (Lapointe et al. 2007). In the Caribbean and Florida, the weevil is a major economic pest due to the larval feeding damage it causes to roots of plants of agricultural (e.g., citrus) and horticultural (e.g. ornamentals) importance (Simpson et al. 1996). Larval damage to roots results in reduced plant growth and exposure to pathogens (Graham et al. 2003). Adults emerge from the subterranean

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pupal chamber and climb onto host plants where they feed, mate, and lay eggs. Field-caught *D. abbreviatus* females can lay over 11,000 eggs during their lifetime (Nigg et al. 2004; Wolcott 1936). Although a variety of control methods have been or are currently being tested (Ulmer et al. 2006; Duncan et al. 2007), none is entirely satisfactory, and this species is still spreading in the United States.

Understanding the reproductive biology of this species in the field may contribute to development of effective control method including efforts to understand the role of semiochemicals in host and mate location (F. Otàlora-Luna, pers. comm.). Despite several decades of research on *D. abbreviatus*, few studies have investigated its mating behavior in field populations. Previous studies showed that the weevils primarily mate diurnally (Schroeder 1981), and are characterized by size-assortative mating (Harari et al. 1999), with a peak in the percentage of individuals mating in the middle of the day (Schroeder 1981). The weevils are attracted to trees that have previously been exposed to weevils of the opposite sex (Schroeder 1981). In captivity, females mate with multiple males (Harari et al. 1999; Sirot et al. 2007), males compete directly for females by attempting to disrupt mating pairs and displace mating males (Harari et al., 1999), and the last male to mate before oviposition fertilizes the majority (~70%) of eggs (Harari et al., 2003; Sirot et al. 2007). However, several characteristics of the mating behavior (e.g., mating frequency, number of mates, etc.) of *D. abbreviatus* in the field are currently unknown. Gaining a more complete understanding of the mating behavior of *D. abbreviatus* in the field will provide information with which to interpret the results of mating studies conducted in captivity and to plan more effective reproductive control methods (Boake et al. 1996).

The goal of this study is to describe the patterns and consequences of *D. abbreviatus* mating behavior in the field. This is the first study of the mating behavior of individually-marked *D. abbreviatus* in the field. We report results on *D. abbreviatus* mating patterns in a commercial plant nursery and follow-up experiments conducted in captivity to clarify the consequences of the patterns we observed in the field.

Materials and Methods

Mating Patterns in the Field

This study was conducted from 7 to 12 May 2002 in a commercial ornamental plant nursery in Homestead, FL (Miami-Dade County). During the study, daytime air temperature ranged between 26°C and 32°C, there was no rainfall, and cloud cover ranged between 0% and 50%. Adult *D. abbreviatus* were collected from 3 neighboring dahoon holly trees (*Ilex cassine*) in the nursery in an area with a high *D. abbreviatus* concentration. On 7 May and the mornings of 8 to 11 May, we collected, marked, and measured 261 individuals of *D. abbreviatus* (115 females, 146 males). We collected the weevils by gently removing them from leaves or branches by hand and recorded their mating status (mating or not at the time of collection). We also measured the length of their right elytra with a dial caliper to the nearest 0.1 mm and marked them uniquely with a 3-dot color code (with uni®Paint Fine Line paint pens) on their pronotum and anterior elytra before returning them to the tree from which they came. From 8 to 12 May, we conducted censuses 4 times per day at 3-h intervals. The 4 censuses began at approximately 0800, 1100, 1400, and 1700 EST and lasted 73.7 min per census on average (SEM: 4.8 min; n = 20 censuses). During the censuses, we searched the leaves, stems, and trunk of all trees within a 5-m × 5-m area centered on the 3 collecting trees. We recorded the activity (standing still, feeding, walking, mating, mounting another, or being mounted) and location of every marked individual re-sighted during these censuses.

It was difficult to confirm actual matings without disturbing the beetles because *D. abbreviatus* engage in intrasexual mountings that appear similar to mating pairs (Harari et al. 2000). For apparent matings in which both individuals were marked, we could verify their sex and whether it was an actual mating by referring to our database of marked individuals. For apparent matings in which the mounting individual was marked but the mounted individual was not marked, we categorized the mounting as mating if the mounting individual was male (as verified by our marking record). For apparent matings in which the mounting individual was not marked but the mounted individual was marked, we categorized the mounting as mating if the mounted individual was female. This definition may have resulted in an overestimate of the actual number of matings, but the overestimate should be minimal because mountings *by* females or *of* males were rare during our study (only 3% and 8% of observed mountings that included 2 marked individuals, respectively). With captive weevils, we assessed both short-term and long-term effects of mating on female fitness, as described in the following sections.

Short-term Effects of Multiple Mating on Female Fecundity and Fertility

We measured the short-term effects of multiple mating by comparing the fecundity and fertility of females mated singly (n = 20) and those mated multiply (i.e., 3 to 4 times, with the same males; n = 20). Adults were collected from the field (University of Florida citrus grove at Ft. Pierce, FL) and maintained in same-sex cages in a greenhouse (natural light cycle; ~27°C) for 2 to 7 d before the start of the experiment. On the first day of the ex-

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periment, we placed individually-marked males and females in pairs (1 male and 1 female/cage) in clear plastic containers (diameter: 10 cm; height: 8 cm; with 1 cm^2 of young citrus leaf, *Citrus macrophylla* Wester). We checked each pair for mating every 30 min. After the pair completed mating, the males were returned to the all-male cage. The females were left in their containers with a piece of wax paper added as an oviposition substrate (Wolcott 1933). On 3 subsequent mornings, we replaced the oviposition substrate in each cage and returned the male partners of females in the multiple-mating treatment to the females' containers. We checked the pairs for mating every 30 min and removed males from cages by 19:00 (EST), by which time all pairs had ceased mating. On the 4th night of the experiment, we removed the males from the mating containers, placed oviposition substrate and fresh citrus leaves in all female containers, and allowed the females to lay eggs for 3 more nights. The wax paper strips and eggs were placed in plastic vials coated with a mist of distilled deionized water in an incubator at 26°C (Lapointe 2001). We counted the number of eggs laid (fecundity) and the percentage of eggs that were fertilized (fertility) for each female.

Our previous research suggested that females receive direct benefits from mating (Sirot et al. 2006). Therefore, multiply-mated females were paired with the same males repeatedly rather than with different males to limit the effects of experimental treatments to those related to mating itself rather than including potential genetic benefits of multiple mating. We used field-caught rather than lab-reared beetles for this experiment because they likely differ in a number of traits that could affect the costs or benefits of mating to females and we were specifically interested in the effects of multiple mating on females in the field.

Statistical Analysis

We used a generalized linear model (GLM) with a Poisson error distribution (Agresti 2002) to analyze the relationship between female fecundity and mating treatment. We used a GLM with a binomial error distribution to analyze the relationship between the percentage of eggs fertilized and the mating treatment. To correct for overdispersion, we used the Williams (1982) method. Female body size and the night that eggs were laid also were included in both analyses. GLMs were performed with the R program (Version 2.2.1; Venables & Ripley 2002).

Long-term Effect of Time Since Mating on Female Fertility

We assessed the fertilization success of females (n = 10) for thee 2-d periods to determine the long-term ability of females to fertilize eggs after a single mating: immediately after mating, 2 weeks after mating, and 4 weeks after mating. We used lab-reared unmated females that had been maintained in an all-female cage for 1 month after eclosion and field-caught males (University of Florida citrus grove at Ft. Pierce, FL) that had been maintained in an all-male cage for 1 week after collection. We used field-caught rather than lab-reared males since these 2 groups of males might differ in the quantity or quality of sperm produced. Females were placed individually in screened cages with a male and with a moistened dental wick and a piece of fresh citrus leaf. At 3-4 h after the start of mating, the mating was interrupted by gently separating the male and female and the female was transferred to a 1-L cage with a wax paper oviposition substrate, a moistened cotton wick, and young citrus leaves (*Citrus macrophylla* Wester). The females were maintained in their individual containers for 2 d and then were placed together in an all-female cage. The oviposition strips and leaves containing eggs from each female were placed in a plastic vial coated with a mist of distilled deionized water in an incubator at 26°C. We counted the number of eggs laid (fecundity) and the percentage of eggs that were fertilized (fertility) for each female. At 2 and 4 weeks after first mating, we again placed each female individually in a 1-L cage for 2 d and collected, incubated, and counted the eggs as described above.

Results

Mating Patterns in the Field

The mean ± SEM length of the right elytron of *D. abbreviatus* collected during our field study was 8.8 ± 0.1 mm (n = 146, range 6.2-11.9 mm) and 10.1 ± 0.1 mm (n = 115, range 7.1-13.7 mm) for males and females, respectively. At the time of capture, 42% of females and 33% of males were mating and there was positive size-assortative mating ($R^2 = 0.15$, $F_{1,46} = 8.03$, $P < 0.01$). Fifty-two percent of males and females were re-sighted at least once during the course of our censuses.

The percentage of marked individuals mating during each census ranged from 39% to 54% for males and 40% to 67% for females. For both males and females, the percentage of individuals mating peaked in the middle of the day (Fig. 1; males: $\chi^2_1 = 2.84$; $P = 0.09$; females: $\chi^2_1 = 3.31$; $P = 0.07$). We observed 28 matings in which both partners were marked and which were not disrupted by our censuses. Sixty-eight percent (19 of 28) of the matings began in the morning and 84% (16 of 19) of these matings ended before the early afternoon (1400 h census). We could estimate mating duration for 17 matings in which both partners were marked. The majority (14 of 17) of these matings lasted <3 h, 1 lasted 3-6 h, and 2 lasted >9 h.

We observed high rates of re-mating by both males and females during our study. We investi-

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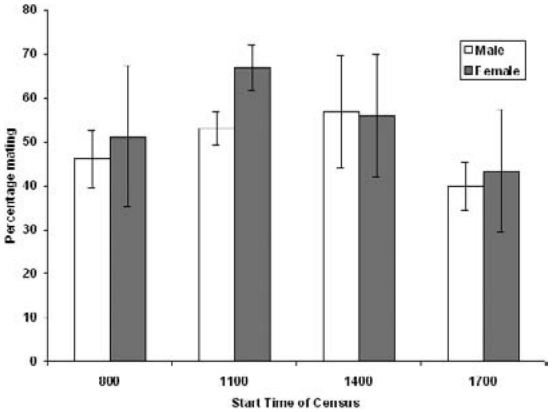


Fig. 1. Percentage (Mean ± SEM) of re-sighted *D. abbreviatus* mating throughout the day in a commercial plant nursery at Homestead, FL (Dade County). Data are based on censuses conducted 4 times per day on 5 consecutive days in May 2002. The percentage of weevils mating tended to peak in the middle of the day for both males and females.

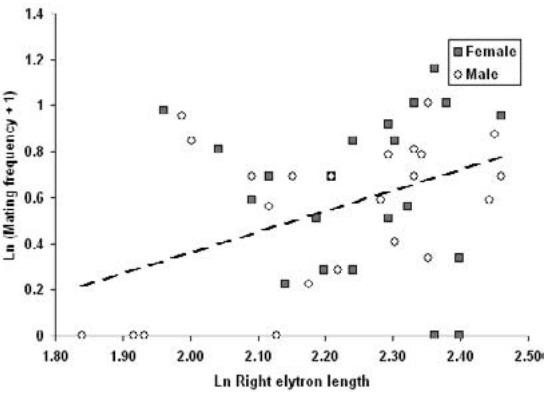


Fig. 2. Relationship between body size and mating frequency of *D. abbreviatus* in a commercial plant nursery at Homestead, FL (Dade County). Mating frequency is the total number of matings by an individual divided by the number of days on which it was observed. Only individuals that were re-sighted on at least 3 d were included in this analysis (n = 21 females; n = 24 males). Dashed line indicates least-squares regression of the natural log of male mating frequency and the natural log of male elytron length. Female mating frequency was not correlated with female size.

gated re-mating patterns for the 21 marked females and 24 marked males that we re-sighted on at least 3 different days. Seventy-five percent of the females mated with multiple partners. On average, females mated slightly less than once per d (0.98 ± 0.12 matings/d; median = 1; range: 0-2.2). Two of 21 females never mated whereas 1 female participated in 11 different matings over the course of the 5-d study. Female mating frequency was not correlated with female size ($F_{1,19}$ = 0.08; P = 0.78; R^2 = 0.004; Fig. 2).

Seventy-six percent of males mated with multiple partners. On average, males mated once every 1.14 ± 0.14 d (median = 1; range: 0-2.25 matings/d). Four of 24 males never mated, whereas 2 males each participated in 8 matings over the course of the study. Male mating frequency was positively correlated with male size ($F_{1,22}$ = 6.7; P = 0.02; R^2 = 0.23; Fig. 2).

For matings that were not disrupted by our censuses, 50% of males and 44% of females whose matings ended before the 1400 h census mated again later the same day. None of the 5 females whose matings ended between the 1400 h and 1700 h censuses were mating with new partners during the 1700 h census, but 3 of them were observed mating the following day. Two of 5 males whose matings ended between the 1400 h and 1700 h censuses were mating with new partners during the 1700 h census and a third male was observed mating the following day. Of the 7 pairs still mating during the last census of the day, 2 females and 5 males were observed mating again the following day.

Of 33 mating pairs in which both partners were marked, 4 (12%) of male-female pairs mated twice during the course of our study. Two of these pairs re-mated on the subsequent d. One pair re-mated 2 d later and 1 pair re-mated 3 d later. For 3 of the 4 pairs, the marked female mated with a different male in between the 2 matings with the marked male.

Of 126 observed mountings *by* marked individuals, 4 were mountings by females and 10 were mountings by males of mating pairs. Of 131 mountings *of* marked individuals, 11 were mountings of males. Intra-sexual mountings did not tend to occur at a particular time of d; such mountings were observed at least once during each of the census times. Mountings of mating pairs by marked males tended to occur in the middle of the day (90% occurred during the 1100 or 1400 censuses), which coincided with the peak of mating activity (Fig. 1). We made *ad libitum* observations of 26 mountings of mated pairs during 2 d of our censuses (10 and 11 May); more of these occurred in the middle of the day than in the early morning and late afternoon (χ^2_1 = 7.54; P = 0.006).

Short-term Effects of Multiple Mating on Female Fecundity and Fertility

The fecundity and fertility of females allowed to mate once or multiple times with the same male were measured over 6 d. Females in singly-mated and multiply-mated treatments laid a similar number of eggs and had similar fertility over all nights of the experiment. Singly-mated females laid a total of 146 ± 34 eggs (range: 0 to 527; n = 20) over nights 2-6 of the study, whereas mul-

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tiply-mated females laid 159 ± 37 (range: 0 to 398; n = 20; GLM; t_{109} = 0.6, P > 0.1; Table 1). The percentage of eggs that were fertilized on nights 2-6 was 86 ± 7% for singly-mated females (range: 0 to 100%; n = 15) and 82 ± 9% for multiply-mated females (range: 0 to 100%; n = 14; t_{54} = 0.7, P > 0.1; Table 1).

Long-term Effect of Time Since Mating on Female Fertility

To determine whether female fertility is sperm-limited, we measured the percentage of eggs fertilized in the first 2 d (n = 10 females), at 14-15 d (n = 7), and at 28-29 d (n = 7) after a single 3-4 h mating. The percentage of eggs fertilized was high in the first 2 d after mating (90 ± 3%), but dropped dramatically by 2 weeks after mating (42 ± 15% Mann-Whitney U test; U =16; P = 0.04, one-tailed test). Only 3 out of 863 eggs laid at 28-29 d after mating were fertilized.

Discussion

Mating Patterns in the Field

Understanding mating behavior of pest species under natural conditions provides essential information for implementing effective control strategies and for designing and interpreting experiments conducted in captivity. Our study established several characteristics of *D. abbreviatus* mating behavior in a field population. (1) Mating duration ranged from <3 to >9 h. (2) Mating activity occurred throughout the day but the percentage of individuals mating tended to peak during the middle of the day, as did mounting of mated pairs by males. (3) Both male and female *D. abbreviatus* mated multiple times and with multiple partners. (4) Male, but not female, mating frequency was positively correlated with body size. (5) Some individuals mated multiple times on different days with the same partner. (6) Mounting by females and mounting of males occurred at low frequencies. Together, these results provide a clearer understanding of the reproductive biology of this important pest species.

The percentage of individuals mating tended to peak during the middle of the day in our study. This pattern was also found in a previous study of *D. abbreviatus* in central Florida (Schroeder 1981), and was suggested to result from an accumulation of mating pairs over the course of the day. Our findings support this hypothesis: matings began throughout the day, but those that began in the morning tended to end by the late afternoon resulting in maximum overlap of matings in the middle of the day. Studies of mating frequency in the field should therefore conduct censuses at consistent times to avoid variation due to diel fluctuations, and should conduct censuses during midday if the goal is to maximize the number of observed matings.

Multiple mating was common for both male and female *D. abbreviatus* at our field site. Over 70% of males and females that we observed participated in multiple matings during the 5-d study. Furthermore, both males and females were observed re-mating within the same day. Re-mating during the same day was also observed in a study of *D. abbreviatus* in captivity (Harari et al. 2003). In that study, mating pairs were interrupted after 2, 4, or 8 h and placed separately in cages with an excess of individuals of the opposite sex. Almost 100% of males and females re-mated later the same day. In contrast, in our study of matings by marked individuals in the field, only 48% of males and 35% of females whose matings ended before the last census were observed to remate later the same day. Our data suggest that although re-mating is common in *D. abbreviatus* in the field, it is unlikely to occur at frequencies as high as those reported from captivity in the Harari et al. (2003) study.

Our study site was characterized by dense aggregations of *D. abbreviatus*. Mating frequency

Table 1. Mean (± SEM) fecundity (number of eggs laid) and fertility (percentage of eggs fertilized) for female *D. abbreviatus* that mated once and those that mated 3 or 4 times with the same male. Neither the fecundity nor the fertility of the 2 treatment groups differed over the course of the study.

Measure	Treatment	Night 1	Night 2	Night 3	Nights 4-6	GLM Results[1]
Number Laid	Singly-mated (n = 20)	56 ± 12	16 ± 5	13 ± 5	118 ± 29	t_{109} = 0.6, P > 0.1
	Multiply-mated (n = 20)	66 ± 15	24 ± 7	8 ± 4	112 ± 29	
Percentage Fertilized	Singly-mated	99 ± 1% (n = 15)	83 ± 10% (11)	99 ± 1% (7)	94 ± 5% (12)	t_{54} = 0.7, P > 0.1
	Multiply-mated	91 ± 7% (14)	94 ± 5% (10)	99 ± 1% (5)	78 ± 11% (12)	

[1]Comparisons of singly-mated and multiply-mated females on nights 2-6.

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may be positively correlated with density. Similar studies of mating frequencies at other field sites are necessary to determine how mating frequency may be affected by density. It is also important to note that we only conducted censuses once every 3 h and may have missed matings. Therefore, our mating frequency results should be treated as minimum estimates of the actual mating frequencies at this site.

Our finding that male mating frequency was positively correlated to male body size suggests that pre-copulatory sexual selection for large male size occurs in the field. The mechanisms underlying pre-copulatory selection for large size are probably competitive ability and mating speed (Harari et al. 1999). Males often obtain matings by competing directly with other males (L.K.S., pers. obs.). Therefore, males who are able to displace other males and obtain matings quickly will have an advantage. In a captive study of citrus grove-collected *D. abbreviatus*, Harari et al. (1999) found that large males displaced smaller males in contests over females and initiated matings more rapidly after mounting. Harari et al. (1999) attributed the latter pattern to female mate choice because females must open their genital aperture in order for males to insert their genitalia. Therefore, both male-male competition and female mate choice are likely to contribute to the mating advantage of large males in the field. If this is the case, then selection may actually be acting on male size relative to other males in the population rather than on absolute male size.

Effects of Multiple Mating on Female Fitness

A pressing question in the field of behavioral ecology is why females mate with multiple males. One hypothesis to explain this pattern is that females may receive direct benefits from multiple matings such as avoiding sperm depletion or receiving substances from the male that increase survival or fecundity of the female or her offspring (Arnqvist & Nilsson 2000). Our previous research on *D. abbreviatus* provided evidence consistent with this hypothesis: male seminal fluid molecules were found predominantly in the ovaries and eggs of mated females (Sirot et al. 2006). In the current study, we tested for direct benefits of multiple matings to females. Our finding that female fecundity and fertility measured over 4 d did not differ for females mated once to a male compared with females mated multiple times to 1 male suggests that female *D. abbreviatus* do not benefit directly from multiple matings in the short-term, in terms of quantity of offspring produced. However, it is still possible that multiple matings (and/or mating to multiple males) result in higher quality offspring or greater female longevity though male-derived resources.

Our results suggest that female *D. abbreviatus* may receive important fertility benefits by repeated matings over the course of their lifetimes. We found that the percentage of fertilized eggs that females lay decreased dramatically with time since mating. This pattern was also observed in a previous study in which females mated with 2 males in rapid succession and were then allowed to lay eggs over 30 d (Harari et al. 2003). Together, these results suggest that female *D. abbreviatus* become sperm-limited when they do not re-mate within 2 weeks after their last mating. Therefore, re-mating by females may function, in part, to replenish sperm stores. Where *D. abbreviatus* are found at low densities, females may benefit by mating with any male they encounter. However, replenishing stored sperm does not seem to be a sufficient explanation for the high re-mating frequency we observed at our field site, which is characterized by a dense aggregation of *D. abbreviatus*. It is likely that females gain additional benefits from mating with multiple males. Edvardson (2007) presents an intriguing possibility that female weevils (*Callosobruchus maculatus*) benefit from access to water provided in male ejaculate during mating. Future research on *D. abbreviatus* should consider similar effects of food and water availability on mating behavior.

In our study, most female *D. abbreviatus* mated multiple times within 5 d. These results suggest that the sterile insect technique (SIT) would not be effective at controlling populations of *D. abbreviatus*, at least at high population densities. Females mated to sterile males readily re-mate with untreated males and the sperm of untreated males are able to fertilize eggs even after a female subsequently mates with a sterile male (Sirot et al. 2007). Our findings that *D. abbreviatus* mate repeatedly in the field and that females may need to re-mate to replenish sperm supplies suggest that males and females seek individuals of the opposite sex multiple times throughout their adult lives and therefore support other researchers' conclusions that sex or aggregation pheromones may occur in this species (Schroeder 1981; Schroeder & Beavers 1985; Harari & Landolt 1997). Future studies should examine whether re-mating behavior and attraction to conspecific odors changes with age or condition. We also found that male mating frequency was positively correlated with male size, suggesting that control strategies that depend on mating success of males should use large males. This relationship remains to be tested for lab-reared *D. abbreviatus*.

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