

# Intrasexual mounting in the beetle *Diaprepes abbreviatus* (L.)

Ally R. Harari<sup>1\*</sup>, H. Jane Brockmann<sup>2</sup> and Peter. J. Landolt<sup>1†</sup>

<sup>1</sup>United States Department of Agriculture—Agricultural Research Service, Gainesville, PO Box 14565, FL 32604, USA

<sup>2</sup>Department of Zoology, 320 Bartram Hall, University of Florida, Gainesville, FL 32611-8525, USA

The weevil *Diaprepes abbreviatus* shows three kinds of same-sex mountings: males mount other unpaired males, males mount males already engaged in copulation and females mount other females. Four hypotheses were evaluated in order to explain same-sex matings by males: (i) female mimicry by inferior males, (ii) dominance of larger males which affects the behaviour of small males, (iii) sperm transfer in which smaller males gain some reproductive success by ‘hitchhiking’ their sperm with the sperm of larger males, and (iv) poor sex recognition. Data from mate choice and sperm competition experiments rejected the female mimicry, dominance and sperm transfer hypotheses and supported the poor sex recognition hypothesis. We tested three hypotheses in order to explain female mounting behaviour: (i) females mimic male behaviour in order to reduce sexual harassment by males, (ii) females mount other females in order to appear larger and thereby attract more and larger males for mating, and (iii) female mimicry of males. The results of our mate choice experiments suggested that the female mimicry of males hypothesis best explains the observed female mounting behaviour. This result is also consistent with the poor sex recognition hypothesis which is the most likely explanation for male and female intrasexual mating behaviour in many insect species.

**Keywords:** mating systems; alternative strategies; reproductive success

## 1. INTRODUCTION

Animals show a variety of mating patterns other than males simply mounting females. Many reports of males mounting other males exist from different animal taxa including insects (Clarke *et al.* 1985; Robertson 1985; Scott 1986; Peschke 1987), snakes (Maynard Smith 1974; Shine *et al.* 2000), birds (Slagsvold & Sætre 1991; Hakkarainen *et al.* 1993; Sætre & Slagsvold 1996) and mammals (Le Boeuf 1974; Fraser & Broom 1997). This behaviour has been variously referred to as ‘pseudofemale’ (Morris 1954*a,b*), ‘homosexual’ (Tuttle 1986), ‘sexual inversion’ (Hinde 1970), ‘female impersonation’ (Norman *et al.* 1999) and ‘transvestitism’ (Vane-Wright 1989; Shine *et al.* 2000), but none of these terms seems appropriate for a behaviour that is a regular part of the male repertoire and that enhances reproductive success. Females mounting other females (which was referred to as ‘pseudomale’ behaviour by Morris (1954*a,b*)) is less common but has been described in lizards (Crews 1987), birds (Hinde 1970) and mammals (Tuttle 1986; De Waal & Lanting 1997; Fraser & Broom 1997). Although female insects have rarely been reported to mount other females (Bagemihl 1999), they have been described as exhibiting male-like colour patterns or male-like behaviour in a number of species including some Odonata (Robertson 1985) and Lepidoptera (Clarke *et al.* 1985). In *Drosophila melanogaster*, females produce male-like pheromones (Scott 1986). Males mounting mating pairs (forming trios) also occur frequently in insects and other taxa, although we could find no specific study of the phenomenon.

Field observations on aggregating adult sugarcane root borer weevils (*Diaprepes abbreviatus* (L.) (Coleoptera: Curculionidae)) (Beavers *et al.* 1982; Jones & Schroeder 1984) have revealed that males mount females, females mount females (Harari & Brockmann 1999), males mount males and males mount mating pairs. When a female mounted a female her ovipositor was extended, as it is during oviposition (Harari & Brockmann 1999) and when a male mounted a male or a pair his genitalia was unsheathed and penetrated the anus cavity.

In order to maximize fitness, an insect may adopt alternative reproductive tactics by making use of various cues (Thornhill 1979) such as the presence of other individuals (Maynard Smith 1974), their size relative to others in the population and the probability that the mating will be disrupted by larger rivals (McLachlan & Neems 1989; Enders 1995; Sigurjonsdottir & Snorrason 1995). An individual male may use one tactic when no competing males are present and a different one when the competition is intense (Forsyth & Alcock 1990). Both male and female intrasexual mounting behaviour may function as an alternative tactic for increasing reproductive success.

### (a) Hypotheses for explaining male–male mounting

Several hypotheses have been proposed in order to explain male–male mounting behaviour.

#### (i) Female mimicry by inferior males hypothesis

Cases of male–male mounting are usually considered as alternative mating tactics that have evolved through sexual selection. They have mostly been interpreted as males mimicking females (Robertson 1985; Scott 1986; Field & Keller 1993; Sætre & Slagsvold 1996). Female mimicry occurs when younger (Hakkarainen *et al.* 1993), weaker or smaller (Laufer & Ahl 1995) individuals mimic the behaviour or pheromones of females in order to avoid

\*Author and address for correspondence: Department of Entomology, The Volcani Center, PO Box 6, Bet Dagan 50250, Israel (aharari@netvision.net.il).

† Present address: USDA-ARS, Wapato, WA 98951, USA.

combat with larger males (Peschke 1987; Laufer & Ahl 1995). Under some conditions this 'making the best of a bad job' tactic may result in some reproductive success (Mason & Crews 1985; Sagi *et al.* 1994). Such behaviour will be favoured by natural selection if these poor-quality males increase their reproductive success by mimicking females.

(ii) *Dominance hypothesis*

Male–male mounting is common among farm animals (Fraser & Broom 1997) and various mammals (Geist 1971) including primates (Tuttle 1986). This behaviour is suspected of being related to male dominance.

(iii) *Sperm transfer hypothesis*

This hypothesis suggests that, in a system where larger males win in male–male competition and fertilize the eggs of larger, more fecund females, small males may exploit the larger male's sperm transfer mechanism. Smaller males may copulate with either a larger male while the latter is in copula with a female or with a large non-mating male. The smaller male's sperm would then be transferred to the female along with the larger male's sperm thus fertilizing some eggs of a female to which the smaller male would not normally have had access. Such behaviour occurs in fishes (Shapiro *et al.* 1994) and some anurans where fertilization is external (Perrill *et al.* 1978), but is rare in internally fertilizing species such as insects (Carayon 1974).

(iv) *Mistake in identifying the female hypothesis*

This hypothesis suggests that lack of a distinct volatile sex pheromone from either sex may affect the ability of males to recognize females (Parker 1968; Sætre & Slagsvold 1992). Males may then use behavioural or morphological cues such as size in order to locate females. Where females are, on average, larger than males, males may initially attempt to mate with a larger conspecific regardless of sex, such as occurs in an aggregating corixid water bug (Aiken 1980).

**(b) Hypotheses for explaining female–female mounting**

Females mounting other females is surprising because it is not a part of a females' typical behaviour. Several hypotheses exist for explaining the advantages for females in showing male-like mounting behaviour.

(i) *Reducing sexual harassment hypothesis*

In some species, male mimicry is thought to reduce sexual harassment of females by males (Robertson 1985; Scott 1986; Cordero *et al.* 1998). If a female looks and acts like a male she may fail to attract males. If male–female sexual interactions are costly for females then selection could favour such male mimicry (Sirot & Brockmann 2000).

(ii) *Acting like a larger individual hypothesis*

Female mounting behaviour may be aimed at attracting better mates. In mating systems where males are attracted by large females and exhibit an active choice for larger females as mates, females may exploit this tendency by either clustering around a large female (hot

shot) or by climbing on a female's back thus looking larger and, as a result, obtaining more or better quality mates than she would have done if she was alone (Beehler & Foster 1988).

(iii) *Male mimicry hypothesis*

As suggested by Harari & Brockmann (1999), when males are highly attracted to a pair in copula and larger males win in the resulting male–male competition over the female, then females may exploit this tendency and obtain larger mates by mimicking a mounting male than if they were to seek a mate alone (Clarke *et al.* 1985; Vane-Wright 1989).

This study will examine the function of two forms of intrasexual mounting behaviour exhibited by adult *D. abbreviatus*: (i) male–male mounting, and (ii) female–female mounting.

## 2. METHODS

**(a) Weevils**

Adult *D. abbreviatus* were collected from ornamental trees near Apopka (Orange County, FL, USA) on nine different occasions during the spring and summer of 1995–1996. Weevils of all samples were sexed in the laboratory (Harari & Landolt 1997). Female *D. abbreviatus* are larger than males (Harari *et al.* 1999) but otherwise show no distinct sexual dimorphism except in the genitalia. In order to assess the size of males and females in the population, we measured the right elytron length of 75 males and 75 females (or all weevils if fewer were collected) collected on each sampling date (measurements made with calipers to the nearest 0.01 mm) ( $n = 1223$  individuals). Males and females were then divided visually into three body size groupings determined by the frequency distribution ( $\pm$  s.e.) of elytron length for each sex (for males small  $< 8.40 \pm 0.01$  mm, medium  $8.40$ – $9.90 \pm 0.01$  mm and large  $> 9.90 \pm 0.01$  mm and for females small  $< 9.90 \pm 0.01$  mm, medium  $9.90$ – $11.00 \pm 0.01$  mm and large  $> 11.00 \pm 0.01$  mm). Weevils of each size category (up to 50 weevils of one sex in a cage) were maintained with green beans for food in different Plexiglas<sup>1</sup> frame cages (30 cm  $\times$  30 cm  $\times$  30 cm) covered on five sides with 1 mm mesh screening and a Plexiglas<sup>1</sup> bottom. Plexiglas<sup>1</sup> cages with males and females were kept in different field cages (3 m  $\times$  3 m  $\times$  3 m) located 50 m apart outside of the USDA-ARS in Gainesville, FL and exposed to outdoor conditions (May–October).

**(b) Male–male mounting behaviour**

Forty females marked with a blue dot (Testors<sup>1</sup> gloss enamel) were placed together with 40 males marked with a green dot (Testors<sup>1</sup> gloss enamel) in a Plexiglas<sup>1</sup> cage (30 cm  $\times$  30 cm  $\times$  30 cm). We recorded the number of males mounting other males and other copulating males (trios) during the 120 min observation period. We also measured the time elapsed from introduction to the minute a male mounted another male ( $n = 51$ ) or a copulating pair (trios) ( $n = 30$ ). Special attention was given to the individual that initiated and ended the mounting.

(i) *Female mimicry by inferior males hypothesis*

The principle prediction of the female mimicry hypothesis is that small males exhibit female-like behaviour in order to avoid combat with larger males. If larger males mounted smaller males then this would support this hypothesis. Therefore, we

first examined the size of the mounting and mounted males by presenting males with a choice of different sizes of males. A random sample of 50 males from each size category in each of three cages (30 cm × 30 cm × 30 cm, as above) were allowed to interact for three days. The animals were observed daily and mounting males ( $n = 51$ ) were marked with a green dot (Testors<sup>1</sup> gloss enamel) while mounted males ( $n = 60$ ) were marked with a yellow dot. The right elytron length of mounting and mounted individuals was measured with calipers to the nearest 0.01 mm. ANOVA with a Tukey comparison (Wilkinson 1997) was performed in order to compare the mean size of mounting males to that of mounted males and to that of the population sampled randomly.

(ii) *Dominance hypothesis*

As in the female mimicry hypothesis, the dominance hypothesis predicts that larger males will mount smaller ones in an act of dominance. Therefore, if larger individuals mounted smaller ones then this hypothesis would be supported, whereas if smaller males mounted larger males then this hypothesis would be rejected.

(iii) *Sperm transfer hypothesis*

We used a sterile male study in order to test the hypothesis that small males transfer sperm to larger males and that these sperm hitchhike along with the larger male's sperm and inseminate a female's eggs. The sterile male study makes use of two males. A female is allowed to mate with one irradiated male and one non-irradiated male. Irradiated sperm are capable of fertilizing eggs but the embryos fail to develop (Boorman & Parker 1976) so the number of eggs that the irradiated male fertilized can be estimated by counting the number of non-developing eggs. In this study only large males were irradiated with X-ray radiation (10 krad<sup>137</sup>Cs at 1200 rad min<sup>-1</sup>). Two experiments using large irradiated males and small normal males were conducted in order to determine whether sperm were transferred (i) during male–male mountings, or (ii) when males mounted copulating males (forming trios). In the first experiment, ten large, irradiated males were kept together with 30 small, normal males ( $n = 3$ ). Small males started to mount and 'copulate' with larger males within 10 min of introducing them into the cage. Surplus, non-mating, small males (Harari & Brockmann 1999) were removed immediately after the first ten males started to mount. When mounting was ceased naturally by one of the males, the irradiated male was taken to a different cage and paired with a receptive female with whom he mated and subsequently guarded in tandem. The mated females were then taken to another cage and were provided with green beans for food and double parafilm sheets (10 cm long and 3 cm wide) attached to the cage wall as substrate for oviposition. Sheets with oviposited eggs were replaced daily for three successive days. The egg-covered sheets were examined for developing embryos after eight days. The presence of viable embryos indicated fertilization by normal sperm, i.e. sperm transferred by the small male to the large male prior to his mating with the female.

In the second experiment, ten large, irradiated males were allowed to copulate and guard ten females for 5 min, after which 30 small, normal males were introduced into the cage. The males mounted the mating pairs thereby forming trios within 10 min and all non-mounting, small males were then removed. The mounting, small males were removed from the cage immediately after they climbed off the male and the remaining large males (irradiated) were allowed to complete

their mating and guarding of the females. Females were then placed in an oviposition cage where they laid eggs as described above. The existence of viable embryos indicated a transfer of sperm from the small male to the larger male while the larger male was mounting the female.

(iv) *Mistake in identifying the female hypothesis*

We tested the hypothesis that male–male mounting behaviour is a result of poor chemical sex recognition, i.e. males use size differences between the sexes rather than pheromones (females on average are larger than males) as a cue for locating females. This hypothesis was tested using two different approaches: (i) an indirect method comparing the size (elytron length) of mounted males and females to individuals in the population, and (ii) a direct method testing the behaviour of males towards larger and smaller individuals regardless of their sex.

In the indirect method we compared the elytron lengths of the following: (i) females in copulation, (ii) females in a field population, (iii) mounted males, and (iv) males in a field population. Mating weevils were collected from unidentified ornamental trees in Homestead, FL on three different occasions in May, August and September 1996. Pairs were gathered by hand from a branch and placed in a vial (2.5 cm in diameter and 5 cm high) with one pair in each vial with two leaves from the host tree ( $n = 201$  pairs). On the same dates aggregated weevils were shaken from branches into a cylindrical box (20 cm × 30 cm) and leaves from the same tree were added as a food source ( $n = 407$  males and 407 females). All weevils were sorted by sex in the laboratory (Harari & Landolt 1997) and the right elytron length of each was measured with calipers to the nearest 0.01 mm. *t*-tests were used to compare the following: (i) sizes of males and females from the field, (ii) sizes of all males from the field with those of mounted males, and (iii) sizes of mounted males with those of mated females. A Kolmogorov–Smirnov two-sample test (Wilkinson 1997) was used to compare the size distribution of each of the above pairs. If (i) the mean size of males was different from the mean size of females, (ii) the mean size of mounted males was different from that of randomly collected males, and (iii) the elytron lengths of mounted males were in the range of sizes of mated females, then the results would support the hypothesis that males have difficulty in recognizing the sexes and may use relative size in searching for females.

In the direct method, we used weevils that were collected from the same orchard in Homestead, FL on 4 August 1998. Aggregating weevils were shaken from branches into a cylindrical box (as above) and leaves from the same tree were added as a food source ( $n = 317$  males and 294 females). The weevils were sorted by sex in the laboratory (Harari & Landolt 1997) and were allowed to adjust to their surroundings (80% relative humidity, 25 ± 1 °C and 16 L:8 D photoperiod) for three days prior to testing. The behaviour of males towards males and females of different size categories was tested.

- (i) In one set of experiments, 11 small males were placed in a Plexiglas<sup>1</sup> cage (30 cm × 30 cm × 30 cm) together with ten large females. A male that mounted either a male or a female was recorded and the pair was removed. All other males and females were then taken back to their cages and a random draw of 11 small males and ten large females was repeated before the next assay. This set of experiments was conducted five times. A total of 41–46 choosing males were used during each set.

- (ii) In a second experimental set, 11 large males were placed in a Plexiglas<sup>1</sup> cage (30 cm × 30 cm × 30 cm) with ten small females. A male that mounted either a male or a female was recorded and the pair was removed. All other males and females were then taken back to their cages and a random draw of 11 large males and ten small females was repeated before the next assay. This set of experiments was conducted five times and a total of 39–49 males were used during each set.

The choice of males was compared with the choice of females after non-mounting individuals (less than 10% in both experiments) were omitted from the data set. *G*-statistics (Sokal & Rohlf 1981) were used for replicates. Tests of goodness of fit were performed for the heterogeneity of the replicates and for the pooled data. Both tests were used to compute the significance of deviations from the expected (1:1) for each experiment.

### (c) *Female–female mounting behaviour*

Observations were made on the mating behaviour of males and females in a Plexiglas<sup>1</sup> cage (30 cm × 30 cm × 30 cm). Forty females were placed together with 40 males with green beans for food. The time elapsed from introduction to the minute a female mounted another female ( $n = 47$ ) was recorded. Special attention was given to the individual that finally mated with the male and to the female that ended the mounting.

#### (i) *Sexual harassment hypothesis*

In order to test the hypothesis that females mount other females in order to prevent sexual harassment by searching males, we gave males a choice between a mounted pair of females and an unmounted female. Five dead (frozen for 48 h) females were glued to the backs of five live females in each of eight cages (this was necessitated by the fact that females mount other females intermittently making it difficult to run choice tests) and were then placed in a cage together with five normal females (with a drop of glue on their backs as a control for the effect of the glue on the male's attraction to females). All females used in this experiment were in the medium-sized category. Ten medium-sized males were introduced into the cage (one male at a time) and their attempts to copulate with either the glued (mounted) females or the unmounted females were recorded. After a choice had been made (defined as climbing on the back of one or the other), the male and the chosen glued female or unpaired female were removed. All other females were then taken back to their cages and a random draw of five glued (mounted) females and five unmounted females was taken for the next assay (this was repeated eight times). A male that did not choose for 10 min was excluded from the experiment. A *G*-replicated goodness of fit test (Sokal & Rohlf 1981) was used in order to test the hypothesis that males did not differ in their choice of either glued (mounted) or unmounted females.

#### (ii) *Acting like a larger individual hypothesis*

The hypothesis that females mount other females in order to attract larger male mates than they would otherwise be able to attract alone predicts that small females will be more likely to mount large females than vice versa. We determined whether there was a size difference between mounting and mounted females. Fifty females from each size category were allowed to interact for three days in each of three cages (30 cm × 30 cm × 30 cm). Mounting females ( $n = 53$ ) were marked with a blue dot (Testors<sup>1</sup> gloss enamel) and mounted

females ( $n = 53$ ) were marked with a red dot during *ad libitum* observations over the next three days. The right elytron lengths of the mounting and mounted individuals were measured with calipers to the nearest 0.01 mm. ANOVA with Tukey honestly significant difference (HSD) multiple comparisons (Wilkinson 1997) was performed in order to compare the mean elytron lengths of mounting and mounted females and a random sample of females from the test population.

In order to test the hypothesis that females mount other females in order to appear larger and, thereby, exploit the male's tendency to choose larger females as mates further, we conducted a choice test. Small and large males were given a choice between mounted pairs of large females and individual large females and a choice between mounted pairs of small females and individual small females. If the female mounting behaviour functions in order to make a pair of females appear larger than they are, then all males, large and small, would be expected to approach and mate with mounted females regardless of their size. To this end, five large, dead (frozen for 48 h) females were glued to the backs of five large, live females (as in §2(c)(i)) and were placed in a cage together with five unpaired large females. Ten large males were introduced into the cage (one at a time) and their attempts to copulate with either glued or unpaired females were recorded. After a choice had been made, the male and the chosen glued female or unpaired female were removed. All other females were then taken back to their cages and a random draw of five glued, large, female pairs and five unpaired, large females was repeated before the next assay. A male that did not choose for 10 min was excluded from the experiment. This set of experiments was repeated with ten small males (one male at a time) ( $n = 8$ ). In a similar experiment, five small, dead (frozen for 48 h) females were glued to the backs of small, live females and were placed together with five small females. Ten small males were introduced into the cage (one at a time) as above ( $n = 8$ ). This set of experiments was repeated with ten large males (one male at a time) ( $n = 8$ ). *G*-replicated goodness-of-fit tests (Sokal & Rohlf 1981) were used in order to test the hypothesis that both small and large males did not differ in their choice of either glued or individual females.

The large size hypothesis, which predicts that mounting females appear larger than non-mounting ones and the male mimicry hypothesis, which predicts that mounting females appear as mounting males (Harari & Brockmann 1999), can be evaluated directly by comparing the responses of large and small males to mounted and unmounted females of different sizes. Small males were expected to respond differently under the two hypotheses. If female mounting behaviour makes a female appear larger, then the mounted female should attract large and small males more often than a similar-sized unmounted female. However, if female mounting behaviour functions in order to make a pair of females appear like a mating couple, with the mounting female mimicking the posture of a mating male, a deceived small male should not be tempted to compete with a larger 'male', but would prefer to mate with a large individual which might be a female.

## 3. RESULTS

### (a) *Male–male mounting behaviour*

Male–male mounting behaviour was frequently observed in the cages. Males walked or climbed over other males ( $n = 368$ ) and sometimes remained on their backs assuming the copulatory posture and extending the

aedeagus ( $n = 64$ ). Male–male mountings lasted  $12.6 \pm 9.5$  min (mean  $\pm$  s.e.) as compared with a maximum of 16 h for male–female mountings (Harari *et al.* 1999). Some individuals attracted more males than others and piles of up to six males, one on top of another, were observed, each one with his aedeagus inserted or making inserting attempts into the male below. Male–male mounting by two males was far more common ( $n = 51$ ) than all other combinations (e.g. piles of three or more males) ( $n = 13$ ). A mounted pair of males separated in one of two ways. Most of the time (39 out of 51 cases) the mounting male fell off when the mounted male started to walk or run, shaking his abdomen from side to side. In some cases, however, the mounting male simply climbed off the other male's back (12 out of 51).

(i) *Female mimicry by inferior males hypothesis*

Contrary to the prediction of the female mimicry hypothesis (that small males exhibit female mimicking behaviour), smaller males tended to mount larger males. When presented with males of different sizes, males mounted more of the larger males than smaller ones and both were different from a random sample of the population (mean  $\pm$  s.e., elytron size of mounted males  $9.004 \pm 0.812$  mm, mounting males  $7.94 \pm 0.100$  mm, random sample  $8.679 \pm 1.048$  mm and range 7.5–11.9 mm) (ANOVA with Tukey HSD multiple comparisons,  $F_{2,525} = 8.506$ ,  $p < 0.001$  and  $n = 528$ ).

(ii) *Dominance hypothesis*

Similarly to the female mimicry hypothesis, the dominance hypothesis can be rejected because it predicts that large males will mount smaller ones. However, when presented with males of different sizes, males were more likely to mount males larger than themselves (see §3(a)(i)).

(iii) *Sperm transfer hypothesis*

The sperm transfer hypothesis can be rejected for both male–male mountings and males mounting copulating pairs (trios) because not one embryo (out of 6990 eggs) developed after a normal male mounted a sterile male that later mated with a female. Furthermore, no normal male that mounted a sterile male in copula resulted in any fertilized eggs (out of 7073 eggs). This means that mounting males are not transferring viable sperm that can be transferred to females.

(iv) *Mistake in identifying the female hypothesis*

The results of the indirect method support the predictions of the hypothesis that males have difficulties with sex recognition and may use size in searching for females (figure 1).

- (i) Males were smaller than females (mean  $\pm$  s.e. elytron size,  $8.679 \pm 1.048$  and  $10.332 \pm 1.148$  mm, respectively and  $t$ -test, d.f. = 812 and  $p = 0.000$ ) (measured as the cumulative size distribution of both groups, Kolmogorov–Smirnov test maximum difference = 0.545 mm and  $p < 0.001$ ).
- (ii) Mounted males were larger than males collected randomly in the field (mean  $\pm$  s.e. elytron size,  $9.004 \pm 0.812$  and  $8.679 \pm 1.048$  mm, respectively, and  $t$ -test, d.f. = 464 and  $p = 0.022$ ) (measured as

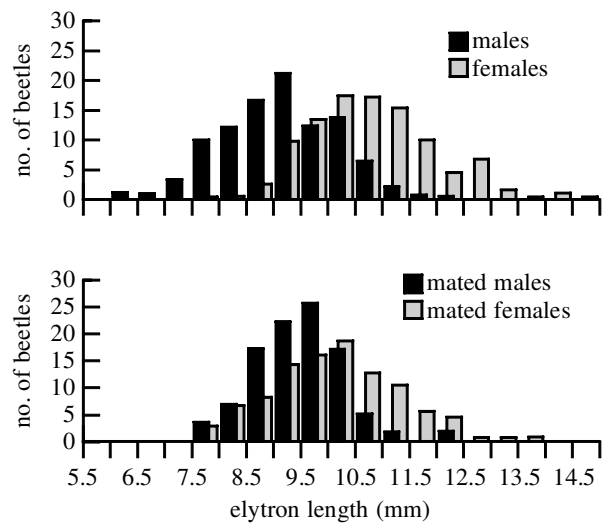


Figure 1. Size (elytron length) frequency distribution of (a) males and females and (b) mated males and females.

the cumulative size distribution of both groups, Kolmogorov–Smirnov test maximum difference = 0.192 mm and  $p = 0.044$ ).

- (iii) The mean size of mounted males was in the range of the sizes of females (range of elytron size of mated males 7.493–10.617 mm and range of elytron size of females 7.493–14.224 mm) and mounted males were smaller than mated females (mean  $\pm$  s.e. elytron size,  $9.004 \pm 0.812$  and  $10.543 \pm 1.287$  mm, respectively, and  $t$ -test, d.f. = 259 and  $p = 0.000$ ). Similarly, the size distribution of the two sexes also differed (Kolmogorov–Smirnov test maximum difference = 0.578 mm and  $p < 0.001$ ) (figure 1).

The results of the direct method support the predictions of the above hypothesis further. Small males presented with a choice of large females and small males were more likely to mount large females ( $88.15 \pm 5.23\%$ ) than small males ( $G_h = 3.55$ , d.f. = 4 and  $p > 0.05$ , and  $G_t = 135.79$ , d.f. = 5 and  $p < 0.05$ ), whereas large males presented with a choice of small females and large males were more likely to mount males ( $74.03 \pm 6.41\%$ ) than small females ( $G_h = 3.77$ , d.f. = 4 and  $p > 0.05$ , and  $G_t = 56.25$ , d.f. = 5 and  $p < 0.05$ ). Even though males were more likely to mount larger individuals *per se*, they mounted more larger females than larger males ( $88.15 \pm 5.23$  and  $74.03 \pm 6.41\%$ , respectively) ( $t$ -test,  $t = 3.871$ , d.f. = 8 and  $p = 0.005$ ), indicating an additional mechanism besides size that may be involved in male mating decisions.

(b) *Female–female mounting behaviour*

Females walked in the cage and frequently mounted other females. When mounting, the female positioned herself along the mounted female's back and extended her ovipositor such that it touched the lower posterior part of the mounted female. The mounted female showed no obvious response and continued to feed or stand. Female mounting lasted  $17.03 \pm 9.6$  min (mean  $\pm$  s.e.). Mounting ceased when either the mounting female climbed off the

other one (17 out of 44 cases) or when a male either touched one of the females or attempted to climb on the pair (27 out of 44 cases). The males mated randomly with either one of the females (13 males mated with the mounting female, 11 males mated with the mounted females and in three cases we did not record which mated). There were no observations of more than one female mounting a female.

(i) *Sexual harassment hypothesis*

Males were more attracted to female–female pairs (glued, mounting females) ( $70.8 \pm 10.9\%$ ) than to unmounted females ( $29.2 \pm 10.9\%$ ) ( $G_h = 6.60$ , d.f. = 7 and  $p > 0.05$  and  $G_t = 23.18$ , d.f. = 8 and  $p < 0.05$ ). This result is not consistent with the sexual harassment hypothesis which predicts that females allow mounting so as to make them less attractive to approaching males.

(ii) *Acting as a larger individual hypothesis*

There was no difference between the elytron lengths of mounting and mounted females (mean  $\pm$  s.e. elytron size, mounting females  $10.325 \pm 0.180$  mm, mounted females  $10.754 \pm 0.161$  mm and random sample of females in the population  $10.332 \pm 1.148$  mm) (ANOVA with Tukey HSD comparisons,  $F_{2,503} = 0.87$ ,  $p = 0.466$  and  $n = 506$ ). However, all females may gain some reproductive success if, by appearing larger, they attract more males. As predicted by the large size hypothesis, large males attempted to copulate significantly more often with either large ( $65.5 \pm 10.7\%$ ) or small ( $64.7 \pm 9.5\%$ ) female–female pairs than with single, large or small females ( $G_h = 4.90$ , d.f. = 7 and  $p > 0.05$ ,  $G_t = 16.27$ , d.f. = 8 and  $p < 0.05$ ,  $G_h = 0.27$ , d.f. = 7 and  $p > 0.05$ , and  $G_t = 16.80$ , d.f. = 8 and  $p < 0.05$ , respectively). However, small males approached and attempted to copulate significantly more often with a single, large female than with large female–female pairs ( $71.7 \pm 8.2\%$ ) ( $G_h = 4.94$ , d.f. = 7 and  $p > 0.05$  and  $G_t = 29.70$ , d.f. = 8 and  $p < 0.05$ ) and were similarly attracted to small female–female pairs and small single females ( $51.7 \pm 8.5\%$ ) ( $G_h = 2.43$ , d.f. = 7 and  $p > 0.05$  and  $G_t = 2.60$ , d.f. = 8 and  $p > 0.05$ ), which was not predicted by this hypothesis.

#### 4. DISCUSSION

(a) *Male–male mounting*

The pattern of male–male mounting behaviour in *D. abbreviatus* is not consistent with the predictions of the female mimicry or dominance hypotheses. According to these hypotheses the mounted male (the female mimic) is expected to be smaller than the mounting (the deceived) male (Andersson 1994). However, mounted males of *D. abbreviatus* are, on average, larger than the mounting ones. This is in contrast with most known cases of female mimicry where the mimetic males are inferior by being younger, weaker (Peschke 1987; Hakkarainen *et al.* 1993) or smaller (Laufer & Ahl 1995) or lacking a valuable resource (Sætre & Slagsvold 1996) but gain from female mimicry by preventing an aggressive attack by a larger male (Laufer & Ahl 1995). Theoretically, it is possible that male quality is not determined solely by size and that large males of low quality could increase their reproductive success by adopting a female mimicry strategy.

However, in our study we did not detect large males of low quality, as was indicated by the large male's rate of winning in male–male competition (Harari *et al.* 1999).

The sperm transfer hypothesis seemed to be a possibility in *D. abbreviatus* because of our observations that (i) small males mounted larger ones, (ii) males mounted mating males (forming trios), and (iii) mounted males inserted their aedeagus into the cavity between the aedeagus and the anus of the mounted male. This hypothesis was ruled out as an explanation for both male–male mountings and males mounting copulating males, since no sperm of any smaller male sired any of the oviposited eggs by females mated with a sterile male during or after an intrasexual mounting. An earlier study (Harari *et al.* 1999) demonstrated that small males transfer sperm easily when mating alone with large or small females.

An alternative hypothesis for both types of behaviour, i.e. males mounting males and males mounting copulating pairs, is the lack of volatile sex attractant from either sex, as suggested by Parker (1968) for the intrasexual mating behaviour of the blowfly *Protophormia terrae-novae*. Poor sex recognition by males is also thought to facilitate the evolution of female mimicry behaviour in pied flycatchers (*Ficedula hypoleuca*) (Sætre & Slagsvold 1992) and male mimicry by females in *Drosophila melanogaster* (Scott 1986). *Diaprepes abbreviatus* individuals of both sexes are equally attracted by male or female volatile chemicals (Harari & Landolt 1997) and males apparently have difficulty recognizing the sex of conspecifics in dense aggregations. However, females are generally larger than males, so size may be used as an indicator of sex. However, since larger males are as large as females (52% of their size distribution is overlapping) (Harari *et al.* 1999) size alone is not a reliable cue. When males mount other males, they prefer males that are above a certain threshold size, which is the size of the smallest female in the sampled population (7.5 mm). The mean elytron size of mounted males (9.02 mm) is in the size range of 89% of the females and only 36% of the males (Harari *et al.* 1999). Males mated with large females more often when large females and small males were presented, but preferred to mate with large males when given a choice of large males and small females. By approaching and mounting a large individual, males increase their chance of mating with a female. However, mistakes are possible when size alone is used as the only cue, for example they might mount a large male. A different way of locating a female is by approaching a mating couple in which one participant is probably a female (same-sex mountings are short lived as compared with males mounting females, which can last for 16 h) (Harari *et al.* 1999). This may explain the occurrence of male attraction to mating couples and the formation of trios (a male mounting a copulating male).

(b) *Female–female mounting behaviour*

Female mounting behaviour has rarely been reported among insects. Female mimicry of males has been suggested as an explanation for females producing a male-like pheromone in *D. melanogaster* (Scott 1986). A similar explanation was suggested in which one form of a polymorphic population of females closely resembles the

male, as in some butterflies (Lepidoptera: Papilionidae) (Clarke *et al.* 1985; Cook *et al.* 1994) and damselflies (Odonata: Coenagrionidae) (Robertson 1985). These phenomena have been interpreted as an alternative reproductive strategy in which females gain an advantage by mimicking the appearance and behaviour of males, thereby escaping excessive sexual harassment by males (Scott 1986; Cook *et al.* 1994; Sirot & Brockmann 2000). The results from our study for female *D. abbreviatus* strongly reject the sexual harassment hypothesis because the female pair attracted more males than did a lone, non-mounting female.

The hypothesis that female–female mounting is a way of appearing larger suggests that females mounting other females may attract more or better quality males by increasing their apparent body size. This hypothesis would predict that female mounting would be particularly common among small females that are unable to compete for or attract the largest males. However, our data showed that this is not the case: there was no size difference between mounting or mounted females. It is of course possible that all females mount other females and, by appearing larger, attract more and larger males than they would have done if they had been alone.

A different hypothesis for explaining female–female mounting, which was suggested by Harari & Brockmann (1999), is that females mount other females and thereby mimic males in copulation (the male mimicry hypothesis). In doing so, a female may attract larger males that will engage in male–male competition, the winner of which will subsequently copulate with one of the females.

In order to determine which of the two hypotheses accounts for female mounting behaviour in *D. abbreviatus* better, the acting like a larger individual hypothesis was contrasted with the male mimicry hypothesis in a series of choice tests. Both hypotheses predict that larger males will be attracted to the mounting females over the single females. However, whereas the acting like a larger individual hypothesis predicts that males of all sizes will be attracted to the large and small mounting females, the male mimicry hypothesis predicts that the large female–female pair will attract only large males. This is because all males prefer larger females as mates, but only large males may win in the resulting competition with the mating ‘male’ and mate with the female. Small males, on the other hand, would rather avoid combat with the large individual and, thus, should prefer to mate with the large female available when given a choice. As expected, in our experiments small and large mounting (glued) females attracted large males, but large mounting females failed to attract small males. Hence, our results further support the male mimicry hypothesis. This means that large males may approach the female–female mounted pair as if they were a mating male–female pair in order to compete with the ‘male’ and take over the female (Harari & Brockmann 1999). Corroborating evidence for this hypothesis comes from the findings that male *D. abbreviatus* are attracted by volatiles of mating couples (Harari & Landolt 1997).

However, contrary to the predictions of the male mimicry hypothesis, we found that small males were equally attracted to small female–female pairs and small non-mating females. However, since small females are, on

average, larger than small males (Harari *et al.* 1999), small mounting females were larger than the males used in the female–female pair experiment. Therefore, small males were probably not as willing as large males to compete with the mounted ‘male’ in the presence of a lone individual that, even though small, was larger than himself. On the other hand, small males did not prefer small females over small mounting females, perhaps because the probability of making a mistake in approaching a small individual as a female when it is actually a male may be quite high.

*Diaprepes abbreviatus* mate in crowded aggregations of up to 100 individuals per 0.5 m<sup>2</sup> with an equal operational sex ratio. Under these conditions a volatile sex pheromone may not be effective in attracting the opposite sex (Landolt 1997). Under these conditions, males can increase their chances of encountering a female by using other cues. Such cues could be the larger size of females and the presence of a female in an already mating couple (Parker 1968; Sætre & Slagsvold 1992).

The male–male mating behaviour observed in *D. abbreviatus* could be a result of males’ inability to tell the difference between males and females when searching for mates. Males mounting copulating pairs (forming trios) could result from the male being attracted by a pair in copula. Female mounting behaviour in this complex mating system could be explained as females exploiting the tendency of males to be attracted to copulating pairs. A female mounting another female may look like a copulating male and should thereby attract males and, since mostly large males approach mating couples, this has the added advantage of ensuring that more large males approach the mounted females (Harari & Brockmann 1999). Bagemihl (1999) listed the published studies of female intrasexual mating behaviour in insects. In all species in which female mounting behaviour occurred, male intrasexual mating behaviour was also found and males had difficulty in distinguishing females from males (LeCato & Pienkowski 1970; Iwabuchi 1987) or conspecifics from closely related heterospecific females (Pinto & Selander 1970). This correlation lends further support to the hypothesis that males use differences in size and the presence of mating couples in identifying females and that females exploit this male behaviour by mounting other females in order to attract larger males.

We thank W. J. Schroeder and H. Smith (USDA-ARS, Orlando, Florida) for supplying laboratory-reared weevils and B. J. Smittle (Division of Plant Industry, Gainesville, Florida) for irradiating the weevils. We also thank V. Chew (USDA-ARS, South Atlantic Area) for advice on statistical analysis and Phil Taylor for his critical comments on the manuscript. This study was supported by postdoctoral fellowship award no. IF-018333-94 from the United States–Israel Binational Agricultural Research and Development (BARD) fund and the Florida Foundation.

## REFERENCES

- Aikin, R. 1980 The relationship between body weight and homosexual mounting in nana Walley (Heteroptera: Corixidae). *Fl. Entomol.* **64**, 267–271.
- Andersson, M. 1994 *Sexual selection*. Princeton University Press.
- Bagemihl, B. 1999 *Biological exuberance. Animal homosexuality and natural diversity*. New York: St Martin’s Press.

- Beavers, J. B., McGovern, T. P. & Adler, V. E. 1982 *Diaprepes abbreviatus*: laboratory and field behavioral and attractancy studies. *Environ. Entomol.* **11**, 436–439.
- Beehler, B. M. & Foster, M. S. 1988 Hotshots, hotspots, and female preference in the organization of lek mating systems. *Am. Nat.* **131**, 203–219.
- Boorman, E. & Parker, G. A. 1976 Sperm (ejaculate) competition in *Drosophila melanogaster*, and the reproductive value of females to males in relation to female age and mating status. *Ecol. Entomol.* **1**, 145–155.
- Carayon, J. 1974 Insémination traumatique hétérosexuelle et homosexuelle chez *Xylocoris maculipennis* (Hem. Anthocoridae). *C. R. Acad. Sci. Paris D* **278**, 2803–2806.
- Clarke, C., Clarke, F. M. M., Collins, S. C., Gill, A. C. L. & Turner, J. R. G. 1985 Male-like females, mimicry and transvestitism in butterflies (Lepidoptera: Papilionidae). *Syst. Entomol.* **10**, 257–283.
- Cook, S. E., Vernon, J. G., Bateson, M. & Guilford, T. 1994 Mate choice in the polymorphic African swallowtail butterfly, *Papilio dardanus*: male-like females may avoid sexual harassment. *Anim. Behav.* **47**, 389–397.
- Cordero, A., Santolamazza Carbone, S. & Utzeri, C. 1998 Mating opportunities and mating costs are reduced in androchrome female damselflies, *Ischnura elegans* (Odonata). *Anim. Behav.* **55**, 185–197.
- Crews, D. 1987 Courtship in unisexual lizards: a model for brain evolution. *Sci. Am.* **257**, 72–77.
- De Waal, F. & Lanting, F. 1997 *Bonobo the forgotten ape*. Berkeley, CA: University of California Press.
- Elgar, M. A. & Pierce, N. E. 1988 Mating success and fecundity in an ant-tended Lycaenid butterfly. In *Reproductive success* (ed. T. H. Clutton-Brock), pp. 59–75. University of Chicago Press.
- Enders, M. M. 1995 Size assortative mating in the tenebrionid beetle of the Namib Desert. *J. Arid Environ.* **29**, 469–484.
- Field, S. A. & Keller, M. A. 1993 Alternative mating tactics and female mimicry as post-copulatory mate-guarding behaviour in the parasitic wasp *Cotesia rubecula*. *Anim. Behav.* **46**, 1183–1189.
- Forsyth, A. & Alcock, J. 1990 Female mimicry and resource defense polygyny by males of a tropical rove beetle, *Leistotrophus versicolor* (Coleoptera: Staphylinidae). *Behav. Ecol. Sociobiol.* **26**, 325–330.
- Fraser, A. F. & Broom, D. M. 1997 *Farm animal behaviour and welfare*, 3rd edn. CAB International (Electronic Publishing).
- Geist, V. 1971 *Mountain sheep: a study of behavior and evolution*. University of Chicago Press.
- Hakkarainen, H., Korpimäki, E., Huhta, E. & Palokangas P. 1993 Delayed maturation in plumage colour: evidence for the female-mimicry hypothesis in the kestrel. *Behav. Ecol. Sociobiol.* **33**, 247–251.
- Harari, A. R. & Brockmann, H. J. 1999 Male beetles attracted by females mounting. *Nature* **40**, 762–763.
- Harari, A. R. & Landolt, P. J. 1997 Orientation responses of the sugarcane rootstalk borer, *Diaprepes abbreviatus* (L.) to weevil, frass, and food odors. *J. Chem. Ecol.* **23**, 857–868.
- Harari, A. R., Handler, A. M. & Landolt, P. J. 1999 Size assortative mating, male choice, and female choice in the curculionid beetle *Diaprepes abbreviatus*. *Anim. Behav.* **58**, 1191–1200.
- Hinde, R. 1970 *Animal behaviour: a synthesis of ethology and comparative psychology*. New York: McGraw Hill.
- Iwabuchi, K. 1987 Mating behavior of *Xylotrechus pyrrhderus* Bates (Coleoptera: Cerambycidae). V. Female mounting behavior. *J. Ethol.* **5**, 131–136.
- Jones, I. F. & Schroeder, W. J. 1984 Capture of *Diaprepes abbreviatus* (Coleoptera: Curculionidae) in frass extract-baited traps in citrus. *J. Econ. Entomol.* **77**, 334–336.
- Landolt, P. J. 1997 Sex attractant and aggregation pheromone of male phytophagous insects. *Am. Entomol.* **43**, 12–22.
- Laufer, H. & Ahl, J. S. B. 1995 Mating behavior and methyl farnesoate levels in male morphotypes of the spider crab, *Libinia emarginata* (Leach). *J. Exp. Mar. Biol. Ecol.* **193**, 15–20.
- Le Boeuf, B. J. 1974 Male–male competition and reproductive success in elephant seals. *Am. Zool.* **14**, 163–176.
- LeCato III, G. L. & Pienkowski, R. L. 1970 Laboratory mating behavior of the alfalfa weevil, *Hypera postica*. *A. Entomol. Soc. Am.* **63**, 1000–1007.
- McLachlan, A. & Neems, R. 1989 An alternative mating system in small male insects. *Ecol. Entomol.* **14**, 85–91.
- Mason, R. T. & Crews, D. 1985 Female mimicry in garter snakes. *Nature* **316**, 59–60.
- Maynard Smith, J. 1974 The theory of games and the evolution of animal conflicts. *J. Theor. Biol.* **47**, 209–221.
- Morris, D. 1954a The reproductive behaviour of the zebra finch (*Poephila gutata*), with special reference to pseudofemale behaviour and displacement activities. *Behaviour* **6**, 271–322.
- Morris, D. 1954b The causation of pseudomale and pseudo-female behaviour: a further comment. *Behaviour* **8**, 46–56.
- Norman, M. D., Finn, J. & Tregenza, T. 1999 Female impersonation as an alternative reproductive strategy in giant cuttlefish. *Proc. R. Soc. Lond.* **B266**, 1347–1350.
- Oberhouser, K. S. 1988 Male monarch butterfly spermatophore mass, mating strategies. *Anim. Behav.* **36**, 1384–1388.
- Otronen, M. 1994 Fertilization success in the fly *Dryomyza anilis* (Dryomyzidae): effects of male size and the mating situation. *Behav. Ecol. Sociobiol.* **35**, 33–38.
- Parker, G. A. 1968 The sexual behaviour of the blowfly, *Prothormia terrae-novae* R-D. *Behaviour* **32**, 291–307.
- Perrill, S. A., Gerhardt, H. C. & Daniel, R. 1978 Sexual parasitism in the green tree frog (*Hyla cinerea*). *Science* **200**, 1179–1180.
- Peschke, K. 1987 Male aggression, female mimicry and female choice in the rove beetle, *Aleochara curtula* (Coleoptera, Staphylinidae). *Ethology* **75**, 265–284.
- Pinto, J. D. & Selander, R. B. 1970 *The bionomics of blister beetles of the genus Meloe and a classification of the New World species*. Urbana, IL: Illinois University Press.
- Robertson, H. M. 1985 Female dimorphism and mating behaviour in damselfly, *Ischnura ramburi*: females mimicking males. *Anim. Behav.* **33**, 805–809.
- Sætre, G.-P. & Slagsvold, T. 1992 Evidence for sex recognition from plumage colour by the pied flycatcher, *Ficedula hypoleuca*. *Anim. Behav.* **44**, 293–299.
- Sætre, G.-P. & Slagsvold, T. 1996 The significance of female mimicry in male contests. *Am. Nat.* **147**, 981–995.
- Sagi, A., Ahl, J. S. B., Danaee, H. & Laufer, H. 1994 Methyl farnesoate levels in male spider crabs exhibiting active reproductive behavior. *Horm. Behav.* **28**, 261–272.
- Scott, D. 1986 Sexual mimicry regulates the attractiveness of mated *Drosophila melanogaster* females. *Proc. Natl Acad. Sci. USA* **83**, 8429–8433.
- Shapiro, D. Y., Marconato, A. & Yoshikawa, T. 1994 Sperm economy in a coral reef fish, *Thalassoma bifasciatum*. *Ecology* **75**, 1334–1344.
- Shine, R., Harlow, P., Lemaster, M. P., Moore, I. T. & Mason, R. T. 2000 The transvestite serpent: why do male garter snakes court (some) other males? *Anim. Behav.* **59**, 349–359.
- Sigurjonsdottir, H. & Snorrason, S. S. 1995 Distribution of male yellow dungflies around oviposition sites: the effect of body size. *Ecol. Entomol.* **20**, 84–90.
- Siro, L. & Brockmann, H. J. 2000 Costs of sexual interactions to females in Rambur's forktailed damselfly, *Ischnura ramburi* (Zygoptera: Coenagrionidae). *Anim. Behav.* (In the press.)
- Slagsvold, T. & Sætre, G.-P. 1991 Evolution of plumage color in male pied flycatchers (*Ficedula hypoleuca*): evidence for female mimicry. *Evolution* **46**, 825–828.



- Sokal, R. R. & Rohlf, F. G. 1981 *Biometry*. San Francisco, CA: W. H. Freeman.
- Thornhill, R. 1979 Male and female sexual selection and the evolution of mating strategies in insects. In *Sexual selection and reproductive competition in insects* (ed. M. S. Blum & N. A. Blum), pp. 81–118. New York: Academic Press.
- Tuttle, R. H. 1986 *Apes of the world, their social behavior, communication, mentality and ecology*. Northridge, NJ: Noyes Publications.
- Wiklund, C. & Kaitala, A. 1995 Sexual selection for large size in a polyandrous butterfly: the effect of body size on male vs. female reproductive success in *Pieris napi*. *Behav. Ecol.* **6**, 6–13.
- Wilkinson, L. 1997. *SYSTAT: the system for statistics*. Evanston, IL: SPSS, Inc.

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