

Male *Megacyllene robiniae* (Coleoptera: Cerambycidae) Use Multiple Tactics When Aggressively Competing for Mates

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Environ. Entomol. 38(2): 425–432 (2009)

ABSTRACT Adult male *Megacyllene robiniae* (Förster) (Coleoptera: Cerambycidae) that are paired with a female often are challenged by conspecific males that attempt to displace them. In staged laboratory bouts, challenging males used seven distinct tactics to displace defending males, including wedging their head between the defender and the female (termed wedging), straddling the mated pair and pulling the defender off (prying), pulling it with the mandibles, batting it with the antennae, or pushing, biting, or kicking the defender. Individual challengers attempted as many as six different tactics in a single bout, repeating certain tactics multiple times. They often attempted tactics that were not very effective. For example, prying was one of the most common attempted tactics but was rarely effective. However, few challengers attempted to push defenders off the female, even though that tactic often was effective. Challengers apparently were influenced by context in their choice of particular tactics. For example, males that approached the mated pair from the side were likely to use wedging, whereas those approaching head on were more likely to bat with the antennae. Choice of tactic apparently was not influenced by absolute size of challengers, nor was it strongly influenced by relative size of defenders. However, the effectiveness of tactics varied significantly with relative body size: larger challengers were most successful when prying or pushing, while smaller challengers were most successful when biting and kicking. By using different tactics, relatively small males were as adept as larger males at displacing rivals.

KEY WORDS mating behavior, interspecific competition, aggression, longhorned beetle

Male animals that are competing for mates may compensate for small body size by adopting alternative mating strategies (Dominey 1984). Cerambycid beetles are appropriate subjects for studying body size effects in mating strategy because variation in nutrition of the wood-boring larvae results in great variation in adult body size (Andersen and Nilssen 1983) and males compete aggressively for females (Linsley 1959). Large males of several cerambycid species have the advantage in aggressive competition for mates, and competition among males results in size-related mating success (Hughes and Hughes 1982; McLain and Boromisa 1987; Edwards and Linit 1991; Goldsmith et al. 1996; Hanks et al. 1996a, b; Wang 2002; Wang and Zeng 2004). In some species of cerambycid beetles, males of different body size adopt very different mating strategies. For example, smaller males may avoid conflicts with larger males by dispersing from areas where conspecific males are abundant, by searching for resources (food plants of adults or larvae) that are

not guarded by competitors, or by intercepting females before they are discovered by larger males (Hughes and Hughes 1982, Goldsmith 1987, Lawrence 1987, Goldsmith and Alcock 1993, Zeh et al. 1992).

In this study, we characterize the mating behavior of the cerambycid beetle *Megacyllene robiniae* (Förster), the locust borer, and present results of experiments that determine how body size of males influences mating success. This familiar species is endemic to eastern North America (Yanega 1996). The diurnal adults are aposematically colored wasp mimics and are active in late summer and fall (Galford 1984, Solomon 1995). Large males can be more than twice the size of the smallest males (range in body length: 11.5–25 mm; Linsley 1964). Adults of both sexes feed on pollen of goldenrod (*Solidago* spp.; Asteraceae) and tend to aggregate on isolated plants with conspicuous inflorescences (Garman 1916, Galford 1984, Harman and Harman 1987). There, males search for females and recognize them by a contact pheromone in their cuticular wax layer (Ginzl and Hanks 2003, Ginzl et al. 2003). Males remain paired with the female after mating, during which time conspecific males will attempt to displace them (M.D.G., personal observation). Females oviposit under loose bark and in cracks in the

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bark of stressed or weakened black locust trees (*Robinia pseudoacacia* L.; Solomon 1995).

We observed during preliminary studies that male *M. robiniae* attempted a variety of tactics to displace rival males that already were paired with females (see below). The great variation in body size of the males suggested that individuals may compensate for small body size by adopting different tactics. In this study, we examine the influence of absolute and relative body size on one component of competition for mates, the ability of unpaired males (challengers) to displace rivals (defenders) that are paired with a mate. We test the following predictions that are based on the current literature on aggressive competition in cerambycid beetles:

Prediction 1: relatively large challengers will dominate in aggressive competition for mates, displacing smaller defenders.

Prediction 2: challengers of different relative size use different tactics.

Prediction 3: challengers choose tactics that are most effective for displacing defenders.

Materials and Methods

Mating Behavior and Aggressive Competition. We characterized the mating behavior of *M. robiniae* and aggressive interactions among males by observing and videotaping ≈ 20 pairs of male beetles that were competing for females on goldenrod inflorescences. This study was conducted at Lodge Park (Piatt County, IL) on sunny and warm afternoons in late September and early October 1997. In many cases, males were obscured by vegetation or their behaviors were not clearly discernible because of the camera angle. Males were clearly visible in five cases, and slow-motion playback of videotapes allowed us to determine which tactics were attempted by challenging males.

Influence of Body Size on Choice of Tactic and Competitive Ability. We tested our predictions by staging bouts between pairs of male *M. robiniae* in three independent laboratory experiments. Adult beetles were collected from inflorescences of goldenrod into glass vials at Allerton Park, Piatt County, IL, within a few days of each study. Body size of beetles was estimated by measuring the length of the right elytron using a caliper. Beetles were housed individually in $\approx 300\text{-cm}^3$ cages of aluminum window screen with fresh goldenrod inflorescences and feeder vials of 10% sucrose solution (glass vial with a cotton roll) that were replaced every 2–3 d. Beetles used in bioassays were vigorous and active in cages.

We conducted our experiments during midday under ambient laboratory conditions. Each bout was initiated by releasing a female into a glass petri dish arena (9 cm diameter, 2 cm tall, lined with filter paper; Whatman No.1, Maidstone, United Kingdom). We introduced one male (the defender) and allowed him to mate with the female. Males always remained in a half mount position with the female after mating (see Results). Immediately after the pair finished mating, a second male (the challenger) was released into the

arena. Body size of challengers (C), relative to the size of defenders (D), was calculated as $(C/D) \times 100$. Challengers and defenders were selected to represent a broad range of relative body sizes. We assigned challengers to three categories based on their relative size: small challengers ($<95\%$ the size of the defender), similarly sized challengers (from 95 to 105% the size of the defender), and large challengers ($>105\%$ the size of the defender). We also explored the data by using more extreme categories (with 10 and 20% differences in relative body size), but these reanalyses did not alter the findings significantly and therefore are not reported here. We also examined the data to determine whether choice of mating tactic was influenced by absolute body size (i.e., small challengers choose different tactics than larger challengers, regardless of the size of the defender).

In each bout, the challenger was allowed enough time to come into contact with the mated pair and one opportunity to separate them (the bout was terminated when the challenger broke off the attack). This limited opportunity for gaining access to a female is representative of natural conditions (see *Mating Behavior and Aggressive Competition*). Individual females were arbitrarily selected and reused in trials. Individual males usually were used in bioassays only once per day, although we reused some males as challengers if they had not mated (but the same two males were never used in more than one trial). Males often were not cooperative, the first male not responding to the female or the second male not challenging the defender. In some cases, challengers apparently did not fight because they had not detected the female, but it usually was not possible to confirm this behavior. On some days, all males were consistently uncooperative. We have noted in studies of the behavior of many species of cerambycids that beetles apparently are influenced by weather conditions, despite the fact that they are under laboratory conditions. For example, males often become inactive when storm fronts are approaching, perhaps because of changes in barometric pressure. We included in our analyses only bouts in which the first male mated with the female and the second male challenged him.

In study 1, we used nine female (mean elytron length \pm SD: 11.9 ± 1.5 mm) and 21 male (10.6 ± 1.1 mm) *M. robiniae* in 49 bouts during 15 September to 8 October 2004 (Table 1). Bouts were videotaped, and we recorded the duration of bouts, the complete sequence of tactics attempted by challengers (including tactics that were repeated within bouts), and the outcome of each bout (i.e., whether the challenger succeeded in separating the mated pair).

Study 2 was conducted by 14 students as a laboratory exercise in an introductory course in entomology (Integrative Biology 460, University of Illinois at Urbana-Champaign) during a 3-h period on 20 September 2005. Seven teams of two students were assigned five male and two female beetles and were allowed to trade beetles as needed to complete 10 bouts each ($N = 70$ bouts). The female and male beetles averaged 11.8 ± 1.0 and 13.4 ± 3.1 mm in elytron length, re-

Table 1. Relative body size (elytron length) of challenging (C) and defending (D) male *M. robiniae* in three independent laboratory studies

Study	Range in relative body size (mean \pm SD)	Number of bouts per size class		
		C < D	C \approx D	C > D
1	70.8–140.5 (105.1 \pm 17.1)	14	18	19
2	81.8–133.3 (101.6 \pm 12.8)	18	22	18
3	59.3–141.2 (101.4 \pm 15.3)	17	25	18

Relative body size = C/D \times 100.

Size classes: C < D, challenger < 95% the size of the defender; C \approx D, challenger 95–105% the size of the defender; C > D, challenger > 105% the size of the defender.

spectively (Table 1). Students were trained to recognize the different tactics of male beetles by the graduate student that had conducted study 1 (A.M.R.). The students recorded the outcome of bouts and which tactics were used by challengers but did not record how many times the same tactic was attempted during single bouts.

In study 3, two undergraduate students used 12 female (11.4 \pm 1.0 mm) and 23 male (15.5 \pm 3.0 mm) *M. robiniae* in 70 videotaped bouts in the laboratory during September and October 2007 (Table 1). The students recorded the same data as in study 2.

We tested prediction 1 (relatively large challengers dominate in aggressive competition for mates, displacing smaller defenders) by calculating the percentage of challengers per size class that succeeded in separating the mated pair. We averaged these percentages across the three studies and tested differences between the means for size classes with analysis of variance (ANOVA).

We first examined the relative rates that challengers attempted the different tactics by calculating the percentage of males (regardless of body size) that used each tactic (excluding repeated attempts of the same tactics within bouts) for each study and calculating the mean. We assessed how effective the tactics were by dividing the number of times each tactic resulted in separating the mated pair by the total number of times it was used (averaged across studies; differences between means were tested by ANOVA, including “tactic” and “study” effects, and the interaction). Differences between pairs of means, for these and subsequent analyses, were tested with the REGWQ means-separation test to control maximum experiment-wise error rates (SAS Institute 2001), and the tests were protected (i.e., means-separation tests were contingent on a significant overall *F*; Day and Quinn 1989).

Because the findings of the three studies were fairly consistent (see Results), we tested prediction 2 (challengers of different relative size use different tactics) by combining the data from all three studies. We calculated the percentage of challengers in each size class that used each tactic and tested differences between size classes with χ^2 goodness-of-fit tests (Sokal and Rohlf 1995; H_0 : percentage for each size class is not different from the mean; *P* value calculated by

Microsoft Excel software). We also conducted a similar analysis using the absolute size of challengers to determine whether choice of tactics was independent of the size of the defender.

We tested prediction 3 (challengers choose tactics that are most effective for displacing defenders) by combining the data for all three studies to calculate the percentage of times that each tactic was effective (i.e., the challenger separated the mated pair) per size class and testing differences between size classes with χ^2 goodness-of-fit tests. This prediction would be further supported if the percentage of males that used a tactic is positively correlated with its percentage effectiveness (tested with the correlation coefficient; Sokal and Rohlf 1995). We tested this prediction separately for each size class of challengers.

We present means \pm SE throughout unless stated otherwise.

Results

Mating Behavior and Aggressive Competition. Male *M. robiniae* moved constantly and quickly through goldenrod inflorescences, so it was very difficult to focus the video camera and characterize their behavior. Males apparently ignored or avoided other males, but whenever they came into contact with an unpaired female, they immediately climbed onto her back, bent their abdomen to connect the genitalia, and appeared to withdraw the ovipositor by extending their abdomen and rearing backward. Females remained stationary while the male rhythmically moved his head up and down with his antennae splayed over those of the female. Within \approx 1 min, the male withdrew his aedeagus and the female began walking with the male in half-mount, holding onto her elytra with his forelegs and walking with his other legs. Some males lashed the female with their antennae, which apparently stimulated her to begin walking. Neither sex seemed to discriminate among potential mates, with nearly every encounter between single males and females resulting in copulation. Individual females mated repeatedly with single males, and with several different males in an afternoon.

Male *M. robiniae* that encountered a mated pair usually would attack the paired male, sometimes resulting in their losing the female or even falling from the plant. Males often had only one opportunity to displace the defending male. In some cases, multiple challengers would assail the defender at the same time. Females showed little response to fighting among males, readily mating with the first male and then with successful challengers. In the field, challengers attempted six distinct tactics in attacking defenders. (1) Challenger climbed onto the back of the defender, grasped the pronotum and abdomen of the defender with his forelegs, and pulled the defender off by extending his hind legs (termed prying). (2) Challenger wedged his head between the bodies of the defender and female, grasping the female's pronotum with his forelegs and attempting to push the defender off by extending his hind legs (wedging). (3) Chal-

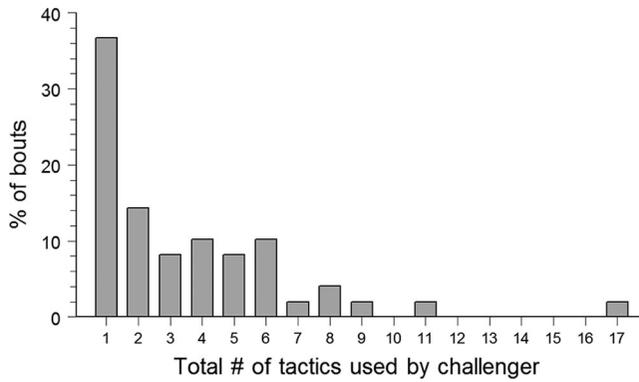


Fig. 1. Frequency distribution of the total number of tactics (including repeats) that challenging male *M. robiniae* attempted against defenders that were paired with a female in individual bouts in study 1 ($N = 49$ bouts).

lenger bit appendages of the defender but did not pull (biting). (4) Challenger pulled on defender's leg with his mandibles (pulling). (5) Challenger used his front legs to push the defender off the female (pushing). (6) Challenger kicked the rival with his hind legs (kicking).

Challengers often attempted multiple tactics, repeating some, in single bouts. Detailed analysis of five video-recorded conflicts between challengers and paired rivals in the field showed the following: (1) challenger attempted (in order) pushing, prying, kicking, and biting, and succeeded in separating the pair, but the female flew away before either male found her; (2) challenger separated the pair by biting the defender and mated with the female; (3) challenger attempted pushing, wedging, pulling, repeated wedging and pulling, but did not separate the pair; (4) challenger attempted pushing but was not successful; (5) challenger attempted wedging but was not successful.

Influence of Body Size on Choice of Tactic and Competitive Ability. In laboratory bioassays, male *M. robiniae* remained with females in the half mount posture after mating. Challengers attempted the same six tactics that were observed in the field, as well as a seventh tactic: batting the defender with the antennae (termed batting). All of these tactics were easily interpretable, with the exception of prying: challengers often appeared to mount the defender by accident and only then detect the defender and attempt to pry him off. It also was difficult to determine whether the challenger was merely clinging to the defender or was actually applying force. Challengers in this position often attempted to mate with the female by bending their abdomen around the defender, which may comprise a completely different strategy, but in many cases apparently was caused by the challenger perceiving the defender as merely an obstacle to mating.

The duration of single bouts between challengers and defenders ranged from 1 s to 4 min (mean \pm SD: 45 ± 30 s) in study 1. More than 35% of challengers attempted only one tactic during individual bouts (Fig. 1), $\approx 50\%$ attempted two to six tactics, and only a few attempted greater numbers of tactics (including

repeats). The maximum was a series of 17 tactics, many repeated, that one challenger attempted against a defender. When considering only the number of unique tactics per bout (ignoring repeats; mean \pm SD across all three studies), $41.5 \pm 16\%$ of challengers attempted only one tactic, and 27.9 ± 9 , 15.8 ± 1 , 12.5 ± 10 , 2.2 ± 4 , 0, and 0% attempted two, three, four, five, six, and seven tactics, respectively.

The three studies were quite consistent in how commonly each tactic was attempted by challengers (indicated by insignificant study and interaction terms in all ANOVAs, below). Tactics attempted most often by challengers were prying and wedging, with the remaining tactics significantly less common (Fig. 2, top; overall ANOVA $F_{8,20} = 5.71$, $P = 0.0038$; tactic term $F_{6,20} = 7.0$, $P = 0.002$). Choice of tactic apparently was influenced by context to some degree. For example, males were more likely to use wedging if approaching the mated pair from the side and batting with the antennae if approaching head on. The tactics varied considerably in how effective they were in separating the defending male from the female (Fig. 2, bottom; overall ANOVA $F_{8,20} = 4.41$, $P = 0.011$; tactic term $F_{6,20} = 5.27$, $P = 0.0071$). Pushing and wedging were the most effective tactics, pulling and batting were intermediate, and the least effective tactics were prying, biting, and kicking. Thus, the choice of tactics did not closely correspond with how effective they were, especially prying, which was quite common but rarely effective. In fact, prying was usually the first tactic that was attempted (Fig. 3), significantly more often than the much more effective pushing tactic, with wedging being intermediate and the other tactics rarely being the first choice (overall ANOVA $F_{8,20} = 4.92$, $P = 0.007$; tactic term $F_{6,20} = 6.56$, $P = 0.0029$).

We did not find support for prediction 1: relatively large challengers did not dominate in aggressive competition for mates. Challengers that were smaller than defenders, similar in size, or larger than defenders were similarly successful in separating the mated pair (mean percent of success across the three studies: 44.6 ± 1.2 , 56.0 ± 1.8 , and $49.1 \pm 11.3\%$, respectively;

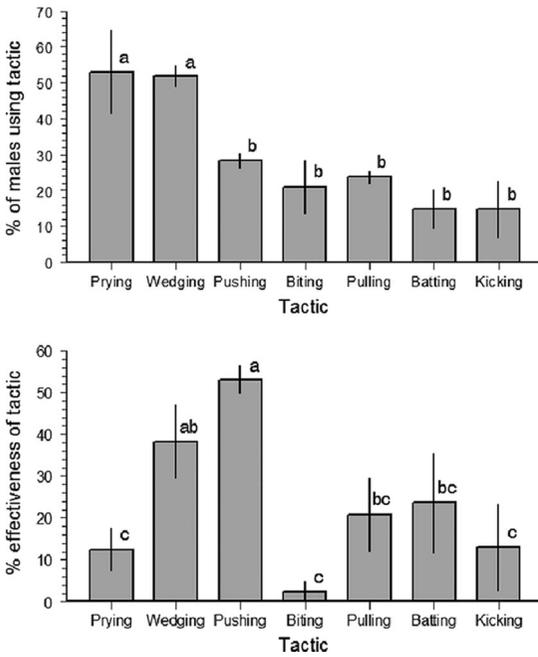


Fig. 2. The mean percentage of challenging male *M. robiniae* (averaged across all three studies) that attempted each of seven tactics against defending males (top) and the mean percentage of bouts in which each tactic was effective in separating the mated pair (bottom). Means for tactics with different letters are significantly different (REGWQ $P < 0.05$).

means not significantly different; overall ANOVA $F_{2,8} = 0.82, P = 0.57$).

There also was little support for prediction 2 (challengers of different relative size use different tactics): similar percentages of challengers in the three size classes attempted six of the tactics (Fig. 4, top; $\chi^2, P > 0.05$). The one exception was pulling, with significantly fewer larger males using it than smaller males (χ^2 statistic = 8.0, $P = 0.018$). In contrast, challengers of different relative sizes differed dramatically in how

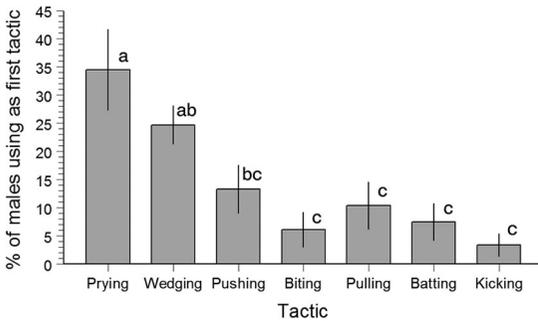


Fig. 3. The mean percentage of bouts in which challenging male *M. robiniae* (averaged across three studies) attempted each of seven tactics as the first tactic in attempting to separate defending males from females. Means for tactics with different letters are significantly different (REGWQ $P < 0.05$).

successful they were in using three of the tactics (Fig. 4, bottom): large size was an advantage in pushing (χ^2 statistic = 10.9, $P = 0.004$), whereas challengers that were similar in size to defenders were most successful with biting (χ^2 statistic = 22.2, $P < 0.0001$) and kicking (χ^2 statistic = 27.1, $P < 0.0001$). The percentage of males that attempted a tactic was not significantly correlated with the percentage effectiveness of the tactic for any of the size classes (correlation coefficient $P > 0.05$), refuting prediction 3 (challengers choose tactics that are most effective for displacing defenders).

Choice of tactic attempted by challenging males also apparently was not influenced by their absolute body size. For example, small males (<9.5 mm in elytron length), medium-sized males (9.5–10.5 mm), and large males (>10.5 mm) attempted prying in 22.2, 24.1, and 26.2% of bouts and wedging in 26.7, 24.8, and 28.5% of bouts, respectively (difference between percentages not significantly different for any tactic, $\chi^2 P > 0.05$).

Discussion

We were surprised by the great number of tactics that male *M. robiniae* had available to them for separating mated pairs. Many of the tactics that male *M. robiniae* used in displacing rivals have been reported for other cerambycid species, including pushing (McCauley 1982, Akutsu and Kuboki 1983), biting (Hughes 1981, Akutsu and Kuboki 1983, Goldsmith et al. 1996, Wang et al. 1996, Iwata et al. 1998), pulling (Akutsu and Kuboki 1983, Hanks et al. 1996b, Møller and Zamora-Muñoz 1997), and kicking (Hanks et al. 1996b). Batting or lashing with the antennae is the most common form of fighting in some cerambycid species that have very elongate antennae (at least 1.5 times the body length; Hughes 1981, Akutsu and Kuboki 1983, Fauziah et al. 1987, Hanks et al. 1996b, Wang et al. 1996, Iwata et al. 1998, Wang and Zeng 2004). The relatively shorter antennae of *M. robiniae* (shorter than the body length; Linsley 1964) may explain why this tactic is not very effective. Males of at least two other cerambycid species use a variety of tactics in aggressive competition for females (McCauley 1982, Akutsu and Kuboki 1983). In fact, males of a congener of *M. robiniae*, *Megacyllene caryae* (Gahan), push and bite paired rivals (Dusham 1921). The two most common tactics of male *M. robiniae*, prying and wedging, have not yet been reported for a cerambycid species to our knowledge. However, males of the cerambycid beetle *Xylotrechus pyrroderus* Bates sometimes mount males that are paired with a female, but in that case, attempt to mate with the male (Iwabuchi 1988).

Also surprising was the number of tactics that male *M. robiniae* would attempt within the brief time that they attacked the defenders, to a maximum of 17 attempted tactics. Males seemed to prefer certain tactics despite the fact that they were not very effective. The possibility remains, however, that our assessment of effectiveness (i.e., whether the mated pair is sep-

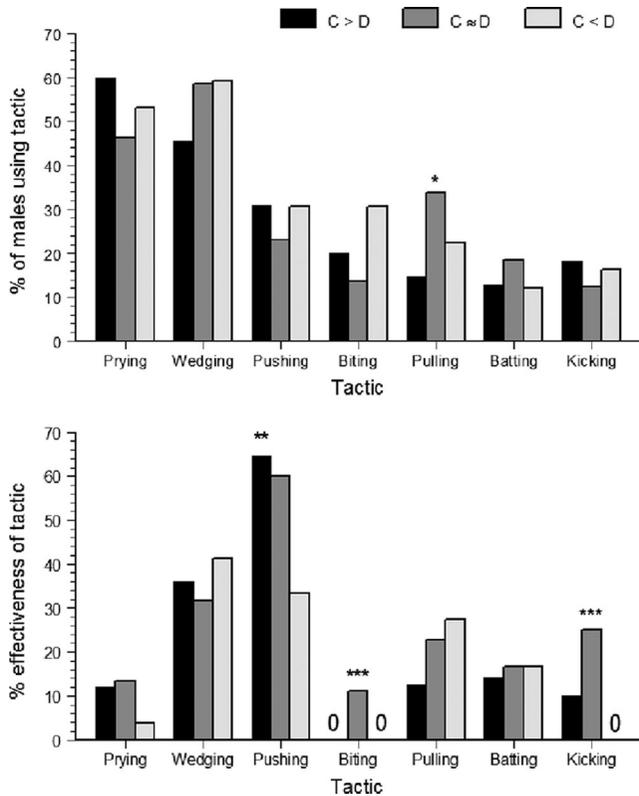


Fig. 4. The percentage of challenging male *M. robiniae* of three relative size classes (data combined for three studies) that attempted each of seven tactics to separate defending males from females (top) and the percentage of bouts in which the tactic was effective in separating the mated pair (bottom). Relative body size (see Table 1) as follows: C < D, challenger < 95% the size of the defender; C ≈ D, challenger 95–105% the size of the defender; C > D, challenger > 105% the size of the defender. * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$, respectively, for significant differences between percentages within tactics (χ^2).

arated) does not consider other benefits for challengers. For example, males may use batting to gauge the body size of competitors (Spieth 1981) and thus avoid resorting to tactics that may result in their being injured. In that case, we would have underestimated the effectiveness of batting. Prying may be relatively common merely because a male that detects the contact pheromone of a female (Ginzel et al. 2003) will instinctively mount whatever beetle is present (including a male that is on top of the female), and once there tries to remove the obstacle by prying. Wedging also may be common because challengers instinctively try to mount the female even though the defender is in the way. The remaining tactics were less common, and choice of these tactics may be strongly influenced by context. Challengers may not have based their choice of tactics on relative size of defenders because they were incapable of accurately assessing body size of other males. The advantage of large body size with the pushing tactic is obvious, but it is difficult to account for the greater effectiveness of biting and kicking for challengers that were similar in size to defenders.

Relatively larger male *M. robiniae* were not more successful in separating mated pairs than were smaller males. This finding is inconsistent with earlier studies

of other cerambycid species that have reported dominance of larger males in aggressive competition for mates (see Introduction), as is true for many types of insects (Thornhill and Alcock 1983). It should be noted, however, that our study was focused on only one component of the suite of behaviors involved in finding females and mating with them. For example, it is entirely possible that larger body size could confer an advantage in searching for mates on goldenrod host plants using contact chemoreception (Hanks et al. 1996a). There also is evidence that male *M. robiniae* produce aggregation pheromones in both their behavior (Lacey et al. 2007) and their having pores on the prothorax that may be associated with pheromone-producing glands (Ray et al. 2006). Body size of males may influence the amount of pheromone they can produce and hence their ability to attract females into their proximity. Variation among males in their ability to produce pheromones therefore also may select for differences between large and small males in the strategies they use in competing for mates.

Mating behavior of *M. robiniae* is consistent with many other cerambycid species (reviewed by Hanks 1999). Lack of discrimination among potential mates

by both sexes seems to be common in this family, with every encounter between the sexes leading to copulation. Male cerambycid beetles commonly remain paired with females after mating, which is advantageous for females of at least some species because repeated mating is necessary for them to reach full fecundity (Akutsu and Kuboki 1983, Khan 1996). Pair bonding may be advantageous for males because it assures the paternity of eggs that are produced during that time, as is true for the cerambycid beetle *Monochamus scutellatus* (Say) and other kinds of insects (Thornhill and Alcock 1983). Male cerambycid beetles therefore may be under strong selection to guard females from other males, particularly for species in which the adults aggregate, as is the case with *M. robiniae*, and aggregations are male biased (Dusham 1921, Hanks et al. 1996a).

Acknowledgments

We thank P. Masonick, M. Knaub, and undergraduate students in the fall 2005 semester of Introduction to Entomology (IB460) at the University of Illinois at Urbana-Champaign (UIUC) for conducting the bioassays. We also thank UIUC for permitting research at Phillips Tract and Allerton Park. Part of this work was in partial fulfillment of a PhD degree for M.D.G. from UIUC. We appreciate funding support from the Alphawood Foundation (to L.M.H.) and the Animal Behavior Society (to A.M.R.).

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Received 19 August 2008; accepted 8 January 2009.
