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**Club Fights in the Weevil *Macromerus bicinctus*  
(Coleoptera: Curculionidae)**

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**ABSTRACT:** Males of the weevil *Macromerus bicinctus* use their elongate forelegs with club-like swellings as "weapons" in ritualized intra-specific contests between males to gain access to females about to oviposit. Fighting and mating behavior are described.

Many features of the external morphology of male animals have been elaborated for fighting conspecific males during social competition for females (e.g., Darwin, 1871; Richards, 1927). Modifications such as horns and enlarged mandibles are often especially striking in beetles. In most of the cases that have been studied, these structures are used as weapons to dislodge or displace rival males of the same species (Eberhard, 1979, 1987 and references therein; Siva-Jothy, 1987; Otronen, 1988).

*Macromerus* is a neotropical cryptorhynchine genus of weevils with 27 described species (Fiedler, 1932). The males of many species differ from the females in having especially long and modified forelegs: the foretibia is curved and swollen at its apex; the first two tarsal segments are broad and covered on their ventral surfaces with dense pads of pale, spreading setae; and the first tarsal segment is disproportionally elongate (Fiedler, 1932). This paper describes how males of *Macromerus bicinctus* Champion use their unusual forelegs both as signalling devices and as weapons during symbolic "fights" which are reminiscent of the "club-fights" of male Yanomamö indians in South America (see Chagnon, 1968).

#### Methods

Adult beetles were active on a fallen log bridging a small stream (Rio Agres) (elevation: ~1500 m) 3-4 km S of San Antonio de Escazú, San José Province, Costa Rica. The log was approximately 12 m long; the tree had been ca. 160 cm in diameter at 1.3 m above the ground when standing. The vegetation bordering the stream was second-growth forest surrounded by open pasture on steep slopes.

The activities of adult beetles were observed on eight different days for a total of approximately 23 hours of observation. All observations were made between 0830 and 1400 in the wet season between 10 June and 19 July 1988. Videotapes were made of 12 aggressive interactions between males (five intense battles), and six courtships and copulations at 30 frames/sec with a National Neveicon Omnipro® camera with +6 closeup lenses. Eleven male beetles were given unique marks with spots of enamel paint on the elytra. Mean values of fight durations are given  $\pm$  one standard deviation.

Voucher specimens are deposited in the British Museum (Natural History) (registration number B.M. 1988-248), the Museo Nacional de Costa Rica, and the Snow Entomological Museum, University of Kansas.

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## Results

**GENERAL NATURAL HISTORY:** As many as 19 males and females were present on the log during the first days of observation, but numbers declined gradually to a single female on 27 July. Two males marked on 11 June were still active 38 days later on 19 July. Females drilled holes and oviposited in them, while males wandered in search of females, copulated, and defended females from the advances of other males. Details of these behaviors are given below.

*Females:* A female typically walked slowly over the surface of the log, stopping frequently to antennate the bark, or probe and bite the surface with her rostrum. In many cases a female began drilling a hole only to abandon the site after a few seconds, or even after more than six minutes. There were no obvious differences between acceptable and unacceptable drilling sites.

A female drilled by gripping the substrate with all her legs and then boring a hole into the wood with her rostrum. The time needed to bore a complete hole, which was as deep as the length of the female's rostrum (see Figs. 1-3), ranged from 690 to 1625 sec ( $\bar{x} = 1114.4 \pm 290.5$ ;  $n = 9$ ).

After finishing a hole, the female removed her rostrum and immediately turned around 180°. After pausing 10-49 sec ( $\bar{x} = 12.8 \pm 5.9$ ;  $n = 23$ ) with the tip of her ovipositor in the hole (presumably ovipositing), the female made a series of tapping or scraping movements with her posterior end. The ovipositor was extended; sometimes it remained inserted into the hole while on other occasions it was removed from the hole, and repeatedly flexed anteriorly with a scraping movement. The significance of these movements is unclear, since when we removed three oviposition sites by cutting out small chunks of wood after the female finished, examination under a microscope showed no signs of secretions or packed materials blocking the hole.

Following this behavior, females usually immediately walked away, but in some cases stood motionless at the oviposition site for <30 sec. In one case a female stayed by a hole for nearly 2 minutes.

*Males:* Males also often antennated and bit or probed briefly at the surface of the log as they moved, but they walked much more rapidly and continuously than did females. They roamed widely, and marked males were observed at various times of the same day at opposite ends of the log.

Searching males usually ignored other solitary males, or tapped each other only briefly with their front legs before moving on. Five pairs of males, however, fought each other when no female was present (duration: range = 4-21 sec;  $\bar{x} = 10.2 \pm 6.6$ ). Apart from fights associated with the presence of females (see below), the only other interactions involving males occurred when one male had his rostrum in a hole in the log, giving the appearance of a drilling female. Another male approached and mounted him in what appeared to be an attempt to copulate, but then quickly dismounted. Approximately 30 sec later a second male approached and repeated the same behavior with the "female-position" male.

**COURTSHIP AND MATING:** Drilling females seemed to be more attractive to males than those which were not actively drilling. Non-drilling females varied in their attractiveness to males. One non-drilling female, for example, stood more or less stationary for nearly 30 minutes and was approached only once by a male which did not even attempt to copulate (two other females less than 10 cm away which



Fig. 1. A marked male *Macromerus bicinctus* rests his front legs, about 4 mm apart, on a female's dorsum as she drills.

were actively drilling had at least four males mate with or fight for them). Occasionally a male mounted a female, then left her without attempting to copulate.

Some females moving along the log were accompanied by males. Usually the male maintained contact with such a female by placing his forelegs on various sites on her dorsum, often on her pronotum with the swollen tibial tips near her humeral angles, and the pair then walked over the log in tandem. The male did not tap or rub his front legs on the female, neither while she was moving nor when she was still, and there was no indication that the modified front legs of the male were used in grasping or courtship. In six of seven cases the males abandoned such moving females within 2 minutes. In the seventh case the male persisted for 18 minutes and then abandoned the female, which showed no signs of attempting to drill.

When a male encountered an unattended drilling female ( $n = 17$ ), or when he successfully displaced another male guarding a female ( $n = 9$ ), he immediately mounted the female, inserted his genitalia, and the pair then copulated for 5 to 28 sec ( $\bar{x} = 12.8 \pm 5.9$ ;  $n = 23$ ). When the male mounted, he usually placed his foretarsi near or on the lateral edges of the proximal part of the female's pronotum, with the tips of his foretibiae near the humeral angles of her elytra. The exact sites where the male held the female varied, however, and the front legs were not moved after gripping her, suggesting again that the male's modified front legs were not used as courtship devices. There were no additional movements during this time other than rhythmic movements of the male's genitalia (e.g.,  $\bar{x} = 1.08 \pm 0.22$  movements/sec in 18 movements by one male). In no case was a male rebuffed even briefly when he attempted intromission.

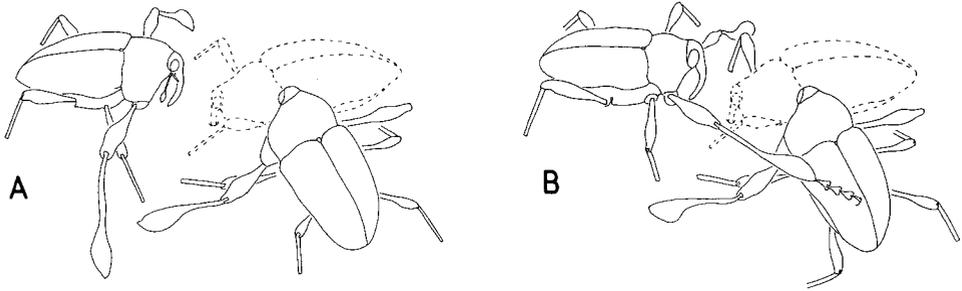


Fig. 2. Males fight near a drilling female (dotted lines—note: rostrum inserted in the log). A) Males are “squared off” (the male on the right evidently did not turn completely to face the other because of the presence of the female). B) 0.27 sec later the male on the left lands a tap on the male on the right with his front leg. (This and the other drawings were made from video images; the tarsi are omitted in most cases because their positions were usually not clear in the video recordings.)

After the male withdrew his genitalia he usually remained with the female until she finished drilling and turned to oviposit, or until he lost a fight to another male. Some males that copulated with non-drilling females, however, left them soon afterward. A male guarded a female by standing nearby, sometimes with his forelegs on her dorsal surface (Fig. 1). In all cases except one, a given male only mated once with the female he was attending. In the exceptional case a male copulated with a female and then guarded for 6 minutes; a second male then approached and fought him. The resident male won the fight, and immediately mounted the female and copulated again. Males usually stopped interacting with females as soon as they ceased drilling and turned to oviposit. Eighteen males left the female as soon as she turned to oviposit; four males remained with a female during part or all of the oviposition, while three males abandoned a drilling female just prior (<60 sec) to the completion of a hole.

**MALE FIGHTING:** We observed 30 cases in which males fought each other by clubbing, and many other less intense battles for access to drilling females; measured durations averaged  $15.7 \pm 11.7$  sec (range = 2–68;  $n = 26$ ). These fights were not significantly longer than those few cases in which no females were present ( $P > 0.5$ , Wilcoxon Two Sample Test). Among 26 cases in which durations were measured, the resident male was victorious 19 times ( $P \cong 0.01$ , with  $\chi^2$ ) after fights lasting from 2–68 sec ( $\bar{x} = 15.3 \pm 16.0$ ). The longest fight was actually more akin to a brawl in which four males participated simultaneously. Seven times the challengers were victorious in fights lasting from 5–39 sec ( $\bar{x} = 17.0 \pm 11.4$ ) (durations not significantly different from those in which challengers lost,  $P > 0.2$  with Wilcoxon Two Sample Test).

A male guarding a female responded to other males when they were up to 7 cm away, turning toward the other animal and moving up to a body length toward him. Sometimes the defending male repeatedly raised his front legs partially, and then set them back down on the log with a sort of stamping or pawing motion before making contact with an approaching male.

In intense fights, males usually tapped each other one or more times with the front legs, then “squared off”, facing each other with their front legs on the log but extended laterally, nearly perpendicular to the longitudinal axes of their bodies

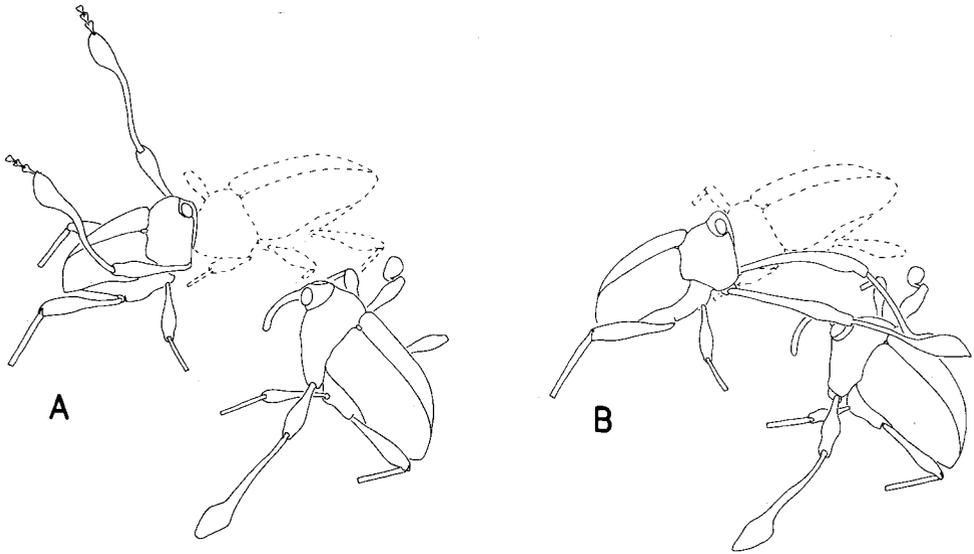


Fig. 3. Males fight near a drilling female (dotted lines). A) Male on the left "cocks" his front legs dorsally. B) 0.67 sec later both front legs have landed in a clubbing movement on the dorsum of the other male. The male on the right had leaned backward following several previous clubbings.

(Fig. 2A). Then (usually) one male tapped the other several times, apparently with the tibiae or tarsi of his front legs (Fig. 2B). A tap involved movements of one front leg more or less directly toward the opponent and, judging by the speed of movement and the *lack* of displacement of the other's body, it did not land with much force. Taps were directed toward various parts of the opponent, including his legs, prothorax, and elytra. In many cases taps seemed to be attempts to pull the other male slightly closer (the opponent's body often rocked forward). Some taps, however, did not appear to function in either of these ways, and in fact it was difficult to distinguish slight repositioning movements of the front legs from taps, especially when the males' front legs were intertwined.

Usually a series of taps was followed by a series of clubbing movements (Figs. 3, 4). The male clubbed his opponent by raising both front legs so they pointed dorsally (Fig. 3A), pausing briefly with his legs raised and his rostrum tucked ventrally against his prothorax, then simultaneously slamming both front legs ventrally onto the opponent (Figs. 3B, 4). In 34 cases it was possible to determine from videotapes which part of the front leg actually hit the opponent: in only eight of them (21%) did the mass at the end of the front tibia strike him; in the others a more proximal portion of the leg made contact (Fig. 4). Clubbing blows were forceful; the downstroke (when the leg was not visible in videotapes) averaged only a single frame. (0.03 sec) ( $\bar{x} = 1.0 \pm 0.3$  frames, giving an approximate velocity at the tip of about 30 cm/sec in 40 blows in three fights). In many cases the opponent's body sagged downward slightly as the blow landed. Males being clubbed often rocked backward slightly (Fig. 3), but otherwise remained nearly motionless. A few clubbing blows ended with the male briefly dragging his front leg across the other's dorsum, causing the opponent to rock forward slightly.

Clubbing blows were usually delivered in series (Fig. 5), with the male imme-

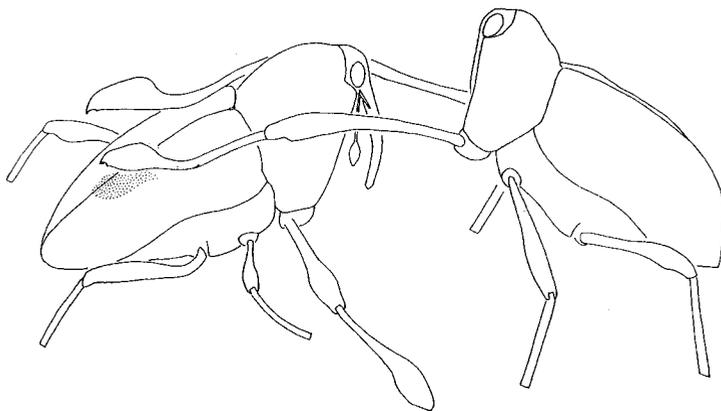


Fig. 4. Male on right lands a clubbing blow on an opponent with his front legs. The curved portions of the tibiae, rather than the enlarged tips, strike the opponent's elytra (note: shadow under male's left tibia).

diately raising his legs again, pausing, and delivering another blow. In five fights the average number/series was  $6.1 \pm 3.3$  (range = 1–12;  $n = 18$ ). The time between blows in a series was relatively constant, averaging  $0.35 \pm 0.10$  sec (range = 0.1–0.6;  $n = 52$ ). In videotapes of three different fights at least one of the males moved the tip of his abdomen dorso-ventrally in a rhythmic manner as if stridulating, but we did not hear any sounds in the field.

Males sometimes raised one or both of their front legs as if to begin a series of taps or slams, then lowered them again without striking the opponent. In some cases a raised leg was moved rapidly (“waved”) without touching the other male before being returned to the substrate.

The sequence of tapping and clubbing in pairs of fighting males varied. Most often one male tapped, then clubbed while the other refrained from moving his front legs (Fig. 5); but sometimes both males tapped or clubbed simultaneously. In the latter case the males alternated in delivering clubbing blows. Careful examinations of videos showed that even during simultaneous tapping and clubbing males showed little indication of movements that appeared designed to parry or ward off the blows of the other.

The longest observed battle lasted more than 155 sec (we saw neither the beginning nor the end), and included at least nine series of clubbing blows (four by one male, five by the other). These males fought near a female under a small, fine-leaved bromeliad plant where their raised front legs repeatedly snagged on the plant's leaves. In this battle each male pushed the other at least once with the dorsal surface of his head; in one case the pushing male also raised his head dorsally at the same time, thus pushing the opponent farther away with his rostrum. Most (but not all) clubbing battles ended while one male was clubbing the other, with the loser turning and walking away while the other continued to hit him (Fig. 5), and occasionally a male even clubbed the log a few times after the other left. This suggests that clubbing usually decides more intense battles.

In less intense battles, one male fled after the other moved or stamped his front legs at him or after only a brief tapping exchange. Usually males of widely differing

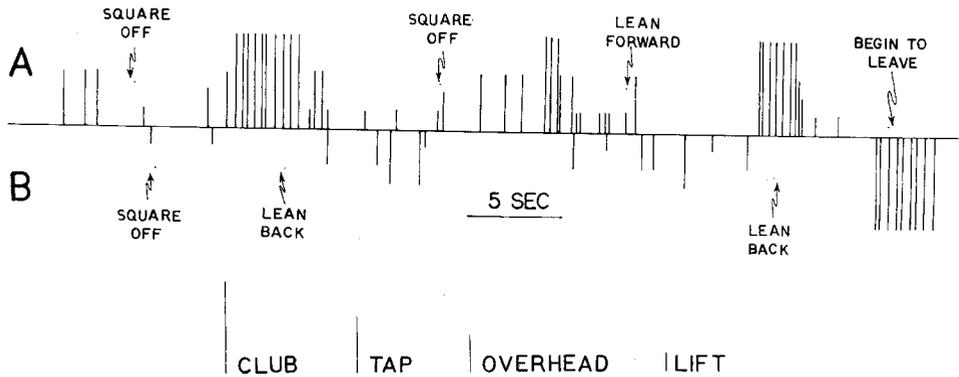


Fig. 5. Movements of front legs by males (*A* and *B*) and other events during the final rounds of the fight illustrated in Figs. 2 and 3. Prior to the behavior shown in the figure, the two males had exchanged blows, and then *B* had turned away to stand over the female. Male *A* then tapped and waved his legs, causing *B* to turn back to face him and continue the fight. The figure depicts the rest of the interaction, in which male *B* withstood three series of clubbing blows before responding with his own series and driving *A* away. CLUB = club with both front legs; TAP = tap the opponent with one or both front legs; OVERHEAD = raise one or both front legs over the head, then lower them without touching the opponent; LIFT = raise one or both front legs less than the height of the body, then lower them without touching the opponent; not included were several minor shifts of position when one of the male's legs touched the leg of the other.

sizes engaged in battles of only low intensity, with the larger male consistently winning. One moderately large male with only one front leg lost all seven fights in which we saw him participate.

### Discussion

There were several indications from the beetle's behavior that the modified forelegs of males function both as threat devices and weapons. In contrast, there was no sign that they serve to grasp or court females.

Male foretibiae are probably designed to function as clubs. Since both a longer lever arm and a larger weight at the tip of the arm will increase the arm's momentum when it is swung, the massive tips of the males' front tibiae and the elongation of the femur and tibia probably evolved to give the leg greater momentum when it is used to club other males. The curvature of the tibia just proximal to the swelling at its tip results in most clubbing blows being struck with the curved section rather than with the tip itself. It is not certain what advantage the curve could bring; it concentrates the force of the impact on a small area of the opponent, and may also insure that the blows strike opponents despite the great length of the front legs.

Clubbing blows were obviously powerful, and the swollen foretibiae of males probably serve to increase the force of the blows. Despite these physical appearances, club fights are probably best considered as symbolic rituals. Clubbing blows never dislodged opponents, and the beetles have such tough cuticle (through which it is difficult to drive an insect pin) that it seems extremely unlikely that the blows cause real damage. Probably the most effective means of directly dislodging an opponent is to use the head to push at and flip the other male by lunging forward and moving the head dorsally, as do some other weevils (Eberhard, 1983), and

as did *M. bicinctus* on two occasions. The observations that males often waited out clubbing attacks by opponents before launching their own (e.g., Fig. 5), and received blows without attempting to parry them, further suggest the symbolic nature of clubbing. In this respect the beetles differ from the male *Yanomamö* mentioned in the introduction, who sometimes severely injure each other in club fights, and the symbolism is presumably learned by others (Chagnon, 1968). Presumably clubbing behavior in *M. bicinctus* is occasionally backed up by more aggression such as pushing, and serves as an indicator of a male's ability to win more direct fights. Our data on this point are only suggestive, however, but similar behavior occurs in other insects (e.g., stalk-eyed flies—Burkhardt and de la Motte, 1987; McAlpine, 1979). Males of some European leaf-rolling weevils (Attelabinae) also have elaborate ritualized contests and fighting behavior between males (Daanje, 1964). In one species (*Byctiscus populi*) males display aggressively by rearing up on their hind legs (II and III), with their forelegs extended outward, parallel to the venter. Males wrestle by grabbing each other with their forelegs, and locking rostra. In another species, *Deporaus betulae*, males display by standing on their mid- and fore-legs, while moving the hind legs. To wrestle each grips the other with the hind legs while the tips of their abdomens are in contact (Daanje, 1964).

In some interactions *M. bicinctus* males raised their front legs without striking blows. It seems likely that the elongate and flattened front tarsal segments covered ventrally with light colored setae function to emphasize the visual stimuli associated with this behavior. These structures, and perhaps also the long legs and swollen tibiae, may function as visual display devices. Daanje's (1964) illustration of a displaying male *Byctiscus* shows that the tarsal setae were also elongate, and similarly may enhance a visual display.

We do not understand why males fold the rostrum ventrally when delivering clubbing blows. Since beetles did not lean forward while clubbing opponents (Figs. 3, 4), it is unlikely that the head is folded to avoid disrupting the blow itself.

Certain behaviors of male *M. bicinctus* suggest that the last male to mate fertilizes the egg (sperm precedence): males tend to guard females during the drilling process and then abandon them at the start of oviposition; they are generally apathetic toward other males in the absence of females; and they aggressively attack them in the presence of females. Other weevils show similar behavior (e.g., *Rhinostomus barbirostris*—Eberhard, 1983), and sperm precedence along these lines has been documented in the weevil *Anthonomus grandis* (Bartlett et al., 1968).

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