

Behavior of adult bottle brush weevils (*Rhinostomus barbirostris*) (Coleoptera: Curculionidae)

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Abstract: Several striking secondary sexual characters of the weevil *Rhinostomus barbirostris* serve as weapons in intraspecific battles between males for females about to oviposit. Smaller males adopt two alternative behavioral tactics in these battles which seem designed to minimize the loss in reproduction which would otherwise result from their inferior fighting abilities. Although the beetles may thus be polymorphic for fighting behavior, there was no sign of morphological dimorphisms. The sizes of their weapons (long rostra) were linearly rather than geometrically related to the sizes of other body parts. The males' behavior suggests that there is strong sperm precedence in this species.

The large weevil *Rhinostomus barbirostris* is relatively common and widespread (Vaurie, 1970); it is an important pest of coconut palms and its general natural history is relatively well known (Wolcott, 1933; Bondar 1940), but surprisingly little is known of the behavior of adult beetles. This study was undertaken to clarify the functions of the striking morphological characteristics of adult males—their elongate front legs and beak, and the thick covering of golden hair on the beak.

MATERIAL AND METHODS

Nearly all of the observations were made during the day in a small patch of forest at the edge of Lago Carimagua near the NE corner of Meta, Colombia in the Holdridgian "dry tropical forest" (Espinal and Montenegro, 1963). The forest consisted mainly of a dense stand of tall palms. Adult beetle activity was observed in May and August of 1978 on recently fallen palm logs for a total of 20-30 hours on 8 different days. The beetles were easily disturbed by nearby movements, and most observations were made by watching events on a given segment of a trunk rather than by following individual beetles. The lower mobility of females permitted some continuous observations however. Individual beetles were marked with distinctive spots of paint on their elytra.

There were often ten to twenty beetles active at any given moment in May, so despite the low number of observation hours, most basic behavior patterns were seen many times. Super-8 movies were made of some behavior, and were analyzed frame by frame.

The observations relating to non-adult life stages were made on a different fallen tree which was dissected with an ax. Other fallen trees in similar patches of forest about 15 km to the north of the study site were also observed. Beetle dimensions were measured with calipers to the nearest .05 mm.

General natural history: The findings of previous authors (Walcott 1933; Bondar 1940) were in general confirmed. Female beetles laid eggs in holes they bored in the trunks of fallen palms, and larvae bored in the interior of the logs. Logs were frequented by adults for only about a month after they fell. Pupation occurred in tunnels which were perpendicular to the log's surface and just below it, and soft, newly molted adults were found in these chambers apparently waiting for their bodies to harden before breaking the thin partition at the surface and emerging. There were no pupation chambers near surfaces of the log which touched the ground, but they did occur on the undersurface of one end of a log which was suspended above the ground, suggesting that gravity was not the cue used by the larvae to

choose sites for pupation chambers. The total cycle from egg to adult was not measured precisely, but in one log it was between 3.5 and 7 months.

The only differences between these and previous descriptions are that the beetles concentrated their activities on fallen rather than standing trees, that they were able to grow to large sizes in some parts of these dead trees, and that adults were active both day and night rather than being strictly nocturnal.

Determination of adult size: Bondar (1940) noted that larvae grew to larger sizes in parts of coconut trunks which were sappier, and thus linked adult size to larval nutrition. Apparent confirmation of this relationship came from measurements of beetles and emerald holes on an old fallen log. The density of both emergence holes (Fig. 1) and tunnels (unquantified pers. obs.) varied along the length of the log, with highest densities in the area just below the crown. The maximum diameters of emerald holes in different sectors were measured, and the holes in less densely populated areas of the log were significantly smaller ($p < .01$, Mann Whitney U Test; Fig. 1). In addition, adult beetles (both males and females) found in their pupal chambers were also significantly larger ($p < .05$, Mann Whitney U Test) in more densely populated areas (Fig. 1a). If the assumption that larvae do not normally move substantial distances along the trunk is correct (the uneven distribution of hole sizes suggests that this may be so, although the interconnecting tunnels in the densely mined central portion of the log suggests that longitudinal displacements were also possible), then these data indicate that large adult beetles are raised from nutritionally superior parts of the log.

An additional pattern was that development of beetles in the more densely populated region of the log was apparently more rapid than that in other parts. At the top end (more than 7m from the base) where the wood was completely honeycombed, the surface was densely pock-marked with emerald holes, and all tunnels were empty. The region between 4 and 7 m had many large larvae, pupae, and teneral adults, while below 3m the tunnels became more sparse, the larvae smaller, and pupae and adults were not present. Assuming that eggs were laid more or less simultaneously (as seems reasonable, given the apparent transient nature of the

logs' attraction to females), these differences imply that not only are beetles from more densely populated regions of the log larger, they also complete their larval development more rapidly.

In common with a number of other wood-inhabiting insects (R. Silberglied, pers. comm.), *R. barbirostris* shows an extraordinary range of adult sizes. In a sample of 65 males, for instance, the largest was about 4 times longer and 20 times heavier than the smallest. Females showed nearly as great a range of sizes (Figs. 1, 2). The relationship between overall beetle size (as indicated by maximum prothorax width) and beak length (from tip to the posterior margin of the eye) was linear in both sexes (Fig. 2). There was no sign that the relationship for large and small males was different (i.e. there was no inflection in the line in Fig. 2) as has been found to be the case with the weapons (horns, mandibles) of other beetles (Arrow, 1951; Kuyten, 1964; Eberhard, 1980; 1982). The relatively larger rostra of males compared to those of females, and the accentuation of the difference in larger individuals was due to the slope of the male line being steeper than the slope of the female line.

Adult behavior: Both males and females were sporadically active, sometimes retiring into holes in the trunk, to the leaf litter under it, or onto nearby vegetation. They consistently retired when rain began to fall, but otherwise I could not discern any pattern to their periods of activity. The beetles seemed to prefer newly fallen logs since one palm which had substantial numbers of adults on it soon after it fell in May was deserted in August when other newly fallen logs nearby had beetles on them. This, in combination with the apparent synchronization of larval development (above), suggests that the beetles produce only a single generation in a given fallen log rather than the series of generations reported by Bondar (1940) on standing coconut palms.

Females: Eggs were laid in the following manner. The female apparently searched for an appropriate site by walking slowly along the log and antennating the surface as she swung her head slowly from side to side. Periodically she stopped and examined a small sector more carefully with her antennae

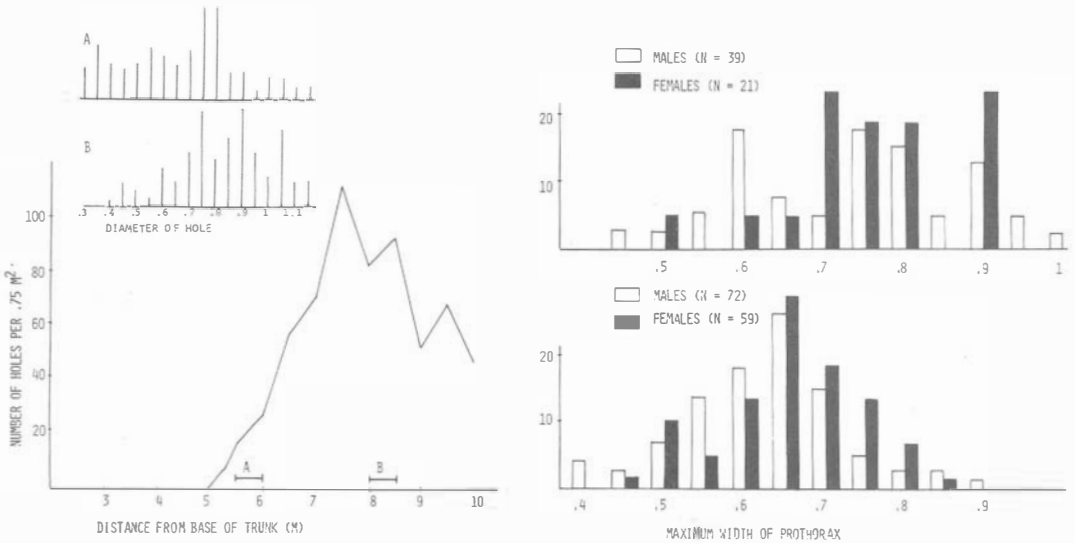


Fig. 1. Relationships of density of larval population with diameters of emerald holes and prothorax widths of teneral adults found in tunnels in the trunk of a fallen palm. There were more holes near the crown of the tree (graph at left). As shown in the inset at left, hole diameters tended to be smaller in a zone of low density (A) than in one of high density (B). The sizes of animals (bar graphs at right) from high density areas (above) were larger than those from low density areas (below).

as she continued to swing her head. Gradually she stopped swinging her head and touched the surface with her mouthparts where drilling would take place while her antennae repeatedly touched the surface nearby. As noted by Bondar (1940), small holes and indentations in the trunk seemed to be particularly attractive. Searching behavior (with lapses of inactivity) lasted from as little as 5 minutes to up to 30 minutes or more (continuous observations of inactive females were not made).

When a site had been found, the female "hooked" herself into drilling position, dragging her legs laterally with the tarsi raised so that the tips of the tibiae hooked the wood (Fig. 3). This behavior evidently served to increase the female's purchase on the log during drilling; one female with a damaged front leg had trouble hooking, and apparently as a result, had difficulty during subsequent drilling.

Once in position, the female normally did not shift her legs again while she used her rostrum to drill a hole (Fig. 4). Sometimes a female abandoned a hole soon after starting and either resumed searching or retired under the log. Drilling was finished after about five minutes, and ended with the female repeatedly bringing her rostrum out of the hole with a

sharp flicking movement, perhaps enlarging or cleaning the opening. Small wood chips accumulated at the sides of the hole during drilling.

When the hole was complete, the female turned 180° to position the tip of her abdomen over the hole, laid an egg into it (logs were not dissected and more than one egg could have been laid; this seems unlikely judging by the sizes of the holes and of mature eggs present in dissected females), and then capped it with a creamy white liquid which very quickly hardened to a brittle consistency. When I tested caps by poking them with the tip of a pencil at intervals of 1, 5, and 15 minutes after oviposition, the material seemed not to harden more, but older caps were much harder. The caps were obviously protective, and one hole whose cap was completely destroyed by my testing had a cluster of small ants around the exposed milky material within 30 minutes, something which was never seen at undisturbed holes.

Deposition of cap material lasted about two minutes, and then the beetle turned 180° and "inspected" the hole, antennating it briefly, and then stood motionless for one to five more minutes before moving on to search for another site or retiring under the log or into a hole.

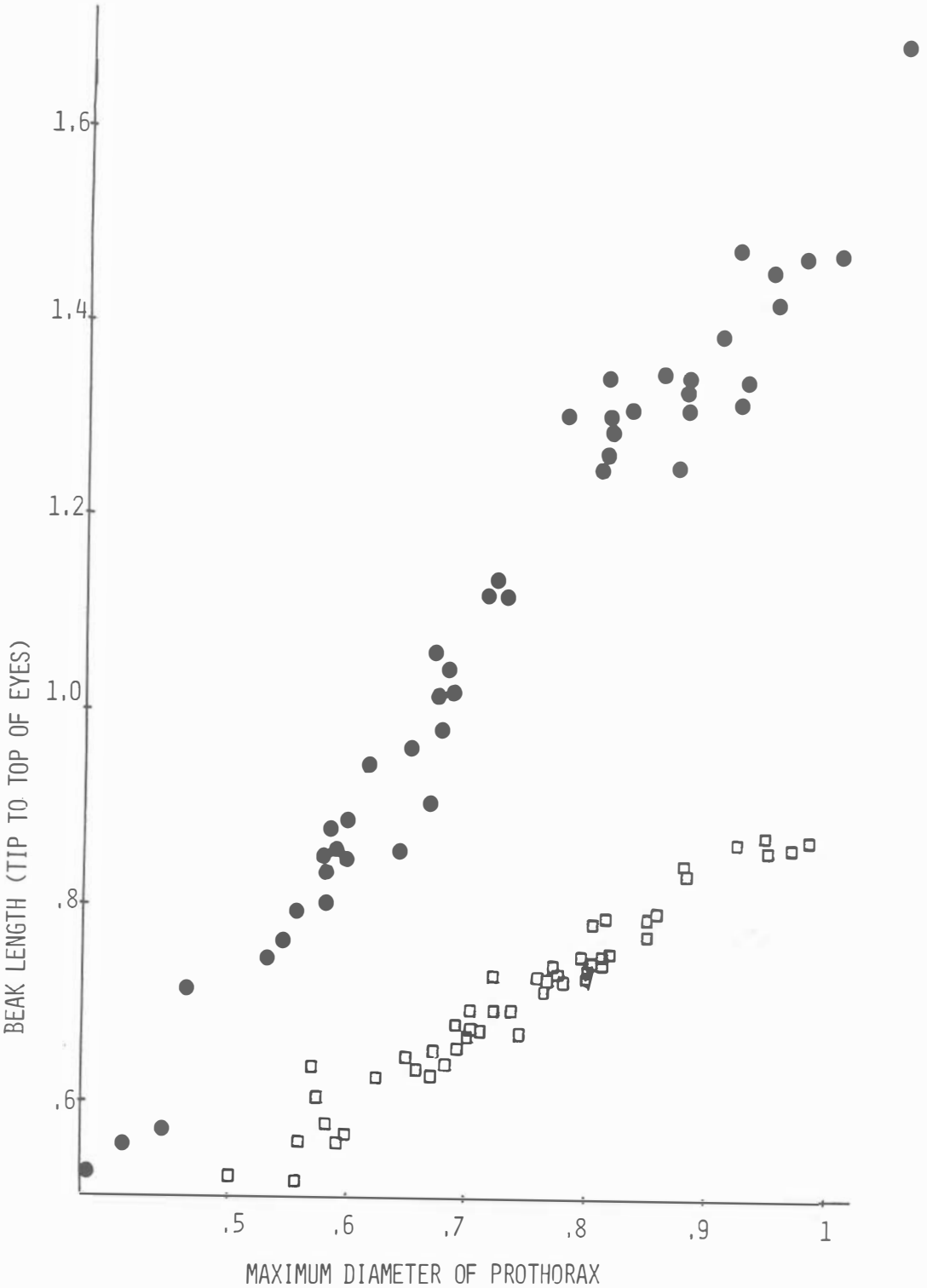


Fig. 2. Relationship between beak length and prothorax width in male (circles) and female (squares) *R. barbirostris*.

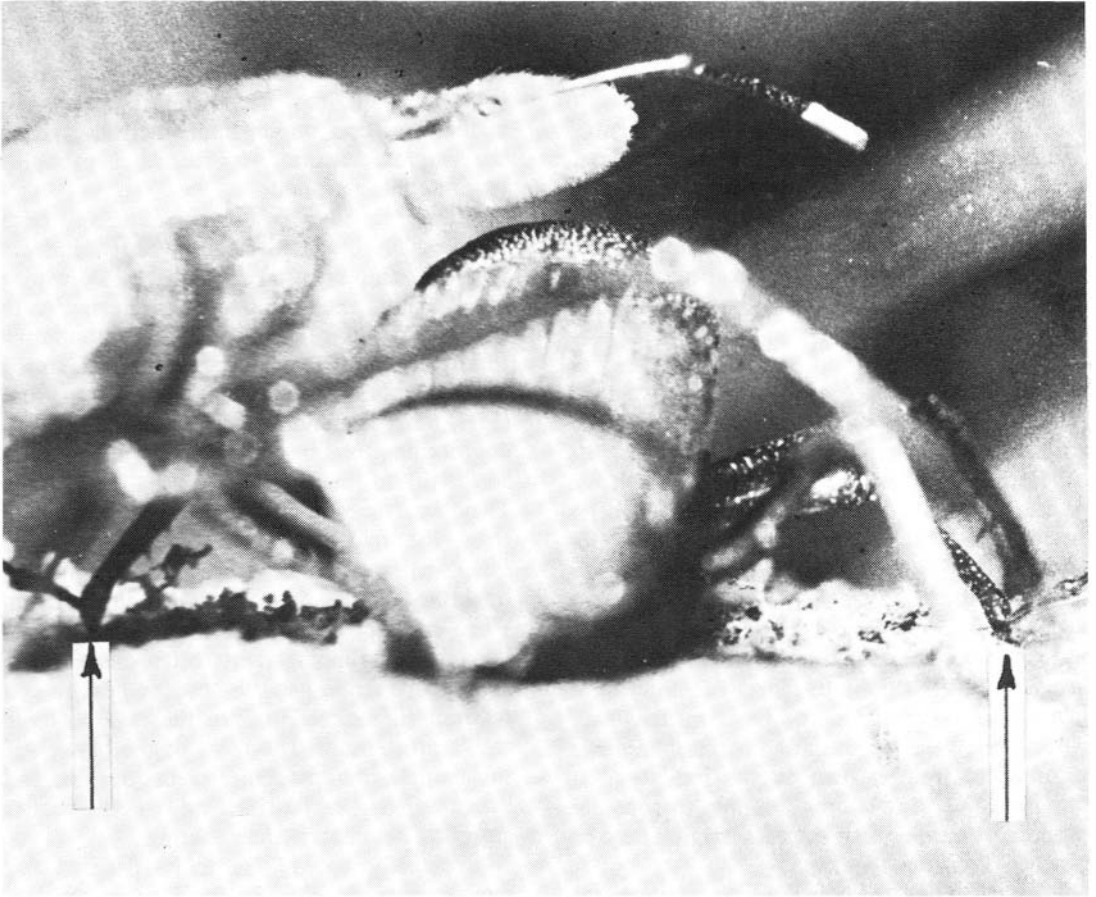


Fig. 3. Female "hookin^g" herself into drilling position using the tips of her tibiae (arrows) (accompanying male out of focus al left).

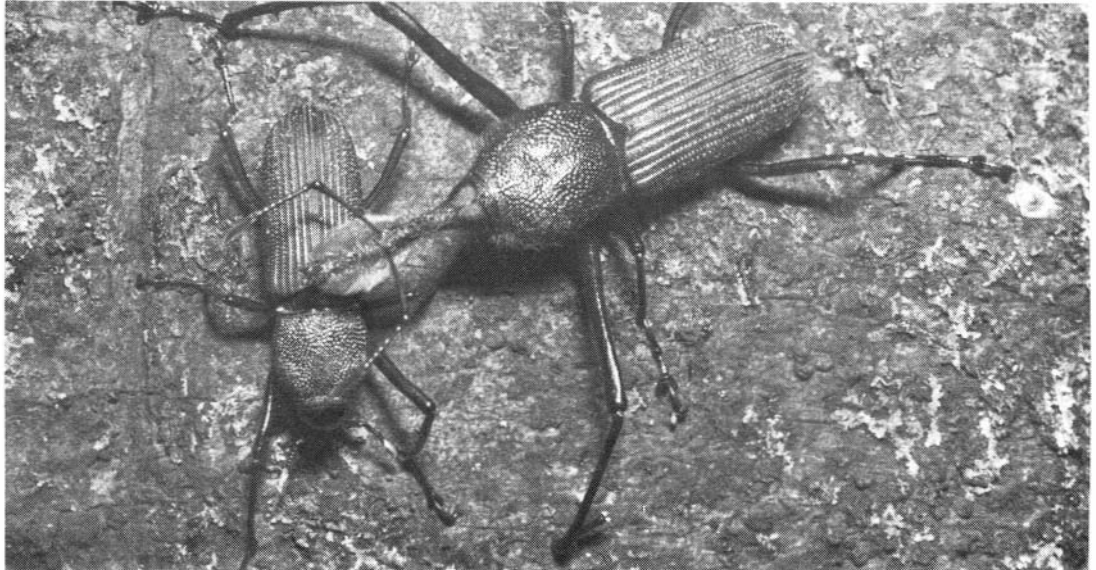


Fig. 4. Female drilling, accompanied by a large male which strokes her dorsal surface with the hairs on his beak.

Females sometimes performed all of these activities alone, but usually they were accompanied by males. They seemed to ignore the males other than to allow mounted males to copulate, although on three occasions a female flipped her head aggressively at a very small male which was trying to insinuate himself under her. Most approaches by other females also elicited aggressive flips from females engaged in drilling or standing near recently laid eggs, and in one case a female knocked another from the log this way.

Males: Males were much more active than females, walking briskly up and down the trunk. Large males moved up to about 10 cm/s or faster, while small males moved at less than a tenth of this speed. When searching males encountered each other, they generally withdrew slightly and/or walked on in slightly different directions; only rarely did they react aggressively. These brief encounters were evidently sufficient to permit recognition of sex, since males' reactions to females (below) were almost always different. One male which encountered the posterior end of another beetle protruding from a hole in the log wiped it assiduously (below) and attempted to copulate with it, suggesting that chemical stimuli may be used to discriminate sex.

A male's first response on encountering a female was nearly always to gently wipe her dorsal surface by moving his rostrum from side to side so that the brush of hair on its ventral surface wiped across her pronotum and/or elytra. In some cases the wiping was only perfunctory, while in others it was more elaborate and was performed sporadically every 15 to 60 seconds for several minutes. Within four minutes (and usually much sooner), the male almost invariably attempted to copulate by mounting the female and applying the tip of his abdomen to hers (Fig. 5). When large males mounted small females it was clear that they stopped wiping the moment they began to attempt genital contact. It was also clear in these and other cases that the female had to open the tip of her abdomen before copulation could occur. The amount of time a male spent tapping against the tip of a female's abdomen with his genitalia before she opened up and allowed intromission varied from a few seconds to 5-10 minutes or more. Some males were not successful despite repeated series of taps

interspersed with dismounts and additional bouts of wiping behavior. In some cases the female began to move away before mating occurred, and the male almost always immediately began wiping more actively, giving the impression that wiping had a pacifying or immobilizing function.

Mating lasted about one minute, and once a male had copulated he dismounted and did not remount, but stayed at her side, wiping occasionally and responding aggressively to the approaches of other males by attempting to knock them from the log with quick, strong flipping motions with his elongate rostrum (Fig. 6). Defending males turned toward approaching males and lowered their heads so the tips of the rostra were near the substrate. They sometimes moved as far as a body length from the female to attack intruders. These other males either moved away or responded by attacking the defenders with their rostra. When rivals of similar size met near a female, long intense flipping fights often ensued. The combatants stood head to head, and exchanged rostrum flips aimed toward the region of the rival's prosternum. The force of the blows was substantial, and sometimes pieces of moss and lichen were ripped from the trunk as the beetles struggled to maintain their footing.

Eventually one of the males desisted and moved away or was knocked from the log. Occasionally both were knocked from the log together and the fight sometimes continued in the litter under the log (this was seen three times) while the female remained unaccompanied and accessible to other males. In less evenly matched encounters, the larger of the two males almost always prevailed. In no case was a male seen to be injured in a fight. Losing males often began searching for other females immediately after being defeated, but other times they returned (sometimes repeatedly) to resume a battle, sometimes even after having been knocked to the ground; in these cases they flew directly to where they had been fighting, demonstrating a surprisingly precise orientation ability. In one extraordinarily intense struggle between two very large males of nearly equal size, one male was knocked from the log five times and the other three, with each returning immediately to resume the fight. Eventually one desisted and he subsequently showed signs of lasting intimidation by passing near the winner several times with-

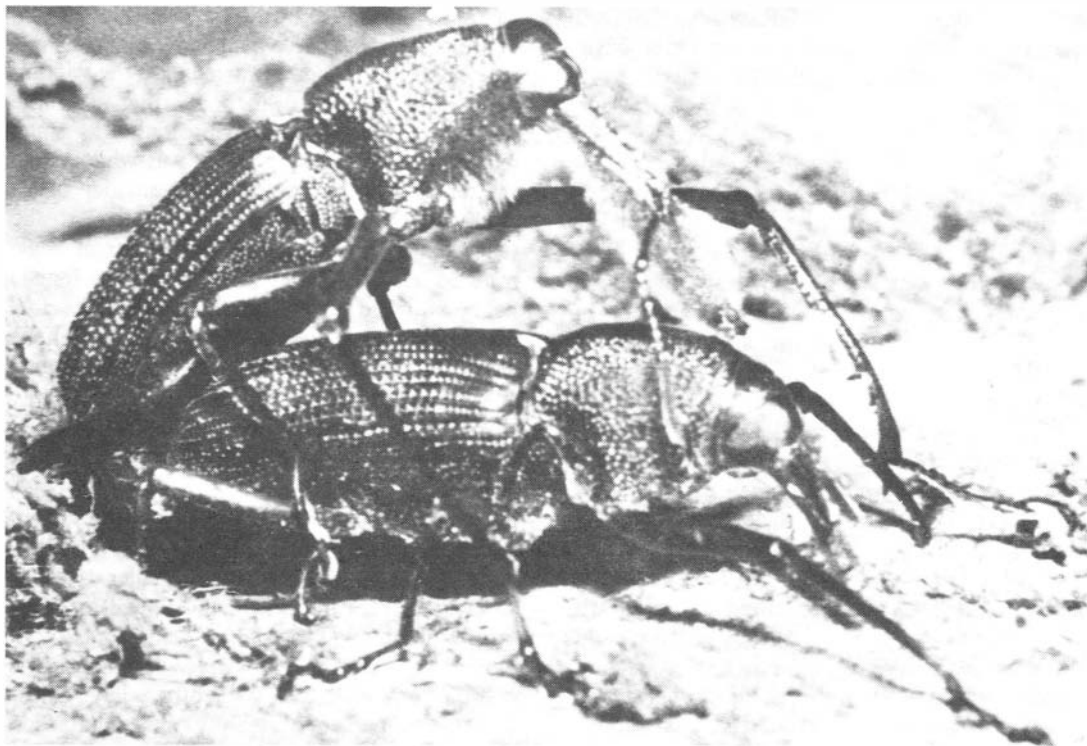


Fig. 5. Drilling female copulating with a male.

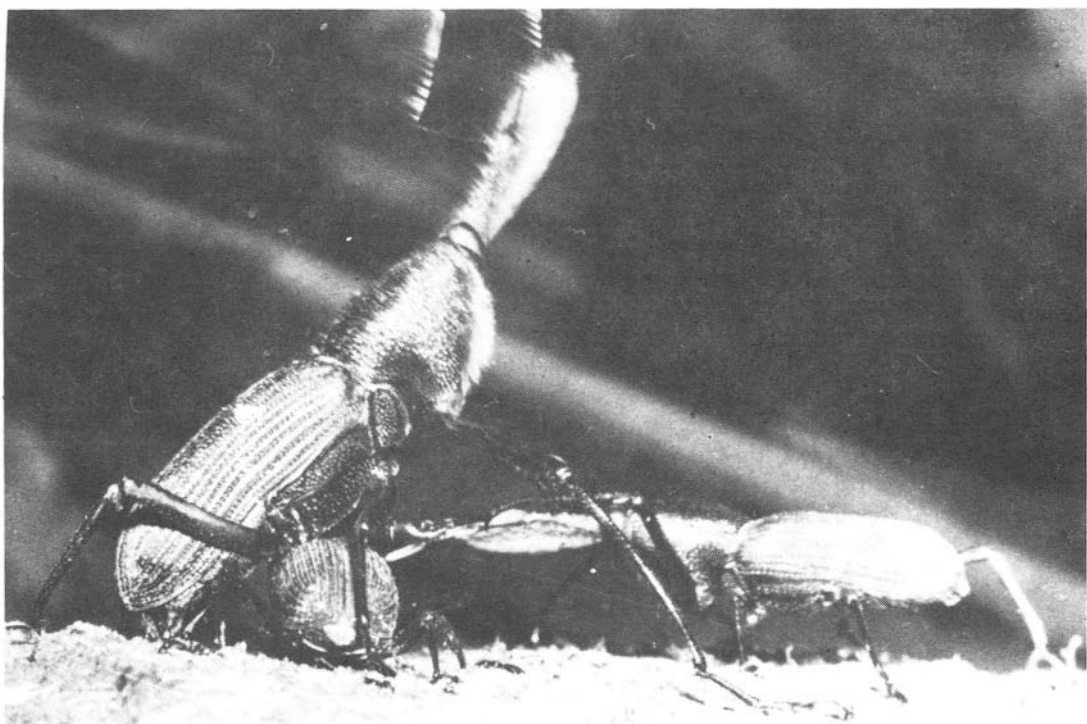


Fig. 6. A large male defending a female against a smaller male. The larger male has just missed the other with an upward flick of his beak. Successful attacks of this kind knock the other male off of the log.

out resuming the fight. Recently defeated males such as this one often showed indecisive, "approach-avoidance" behavior, starting to walk away only to pause and/or veer back toward the disputed female.

Every time one male succeeded in supplanting another beside a female, he tried to copulate with her either immediately or after a brief period of wiping. Since there were always more males than females active on a log at a given moment, this meant that in the 5-10 minutes preceding an oviposition a female often copulated with a series of males of increasing sizes. The last male usually stayed until about one minute after the female turned to oviposit, then stopped wiping and walked away. Occasionally a male stayed with a female during oviposition and post-oviposition "inspection" and moved with her as she moved off to search for a new drilling site. In these cases the male did not remount the female. Males which left females were still sexually active, and sometimes found and mated with a second female within a minute or less of leaving.

Some females were relatively unattractive to males, and were passed by or given only brief inspections by patrolling males. Some of these females were inactive, and neither searched nor drilled, while others consistently refused copulation attempts. One had an injured leg and was unable to hold herself in position to drill. In general, females engaged in drilling were attractive to males. Some immobile females were also attractive however, and some recently rejected females were subsequently joined by other males. It was not clear what cues were being used by the males to select among non-drilling females.

Two types of variations of the typical male aggressive behavior described above were noted on several occasions. In some fights in which a relatively small but not tiny resident male was challenged by a larger rival, there was a brief interchange of flipping behavior and the resident ended up clinging to the body of the other. The larger beetle was usually unable to bring his rostrum to bear on his opponent, and despite continued struggles was thus at least temporarily powerless to dislodge him. This clinging behavior of the smaller male may constitute a "delaying action" designed to distract or impede the larger (and inevitably victorious) male from copulating with the female for long enough to permit the female

to finish drilling and begin oviposition. In two of the six cases in which this behavior was observed, this indeed occurred, and the winning male only succeeded in copulating after the female had turned and oviposited. The small male thus effectively won the war while losing the battle. In two other cases smaller males clung tightly to the female rather than to the rival male, and the flips of the larger male resulted in both the small male and the female being knocked to the ground under the log. The smaller male then accompanied the female as she climbed back onto the log and searched for a new drilling site. Clinging behavior like this was never seen to be performed by males which were larger than or equal in size to their opponents.

A second alternative tactic, seen on eight occasions, was performed only by very small males. In general these dwarf males (Fig. 6) were usually easily chased or flipped away by larger guarding males. They were able to get close to guarded females however during the commotion of battles with other, large males by combining slow, stealthy movements and their small size to hide from their rivals. The following description of a successful use of this tactic is typical. A dwarf male moved in close to a male-female pair as the male turned to flip at another passing male. The dwarf stayed immobile, close to the side of the female's thorax, and the guarding male appeared not to notice him. The guarding male was then replaced by a larger one after a brief fight during which the dwarf flattened himself to the trunk. The new male mounted and copulated with the female, and then stood by her side (opposite to the dwarf) and wiped her dorsum. The dwarf slowly edged backward until he was at the tip of the female's abdomen, where he wiped briefly and then mated while the larger male continued wiping (Fig. 7). Within a short time the female turned to oviposit, and both males left. This was the only successful try of eight such interactions I observed involving dwarfs. No larger males were ever seen to use this kind of behavior, and dwarfs were never seen acting aggressively, even when two dwarfs encountered each other on the same female, so it seems probable that this is a separate tactic designed to function for dwarf males.

The following typical scene on a fallen palm serves to summarize the observations of adult behavior. There are several male-female pairs

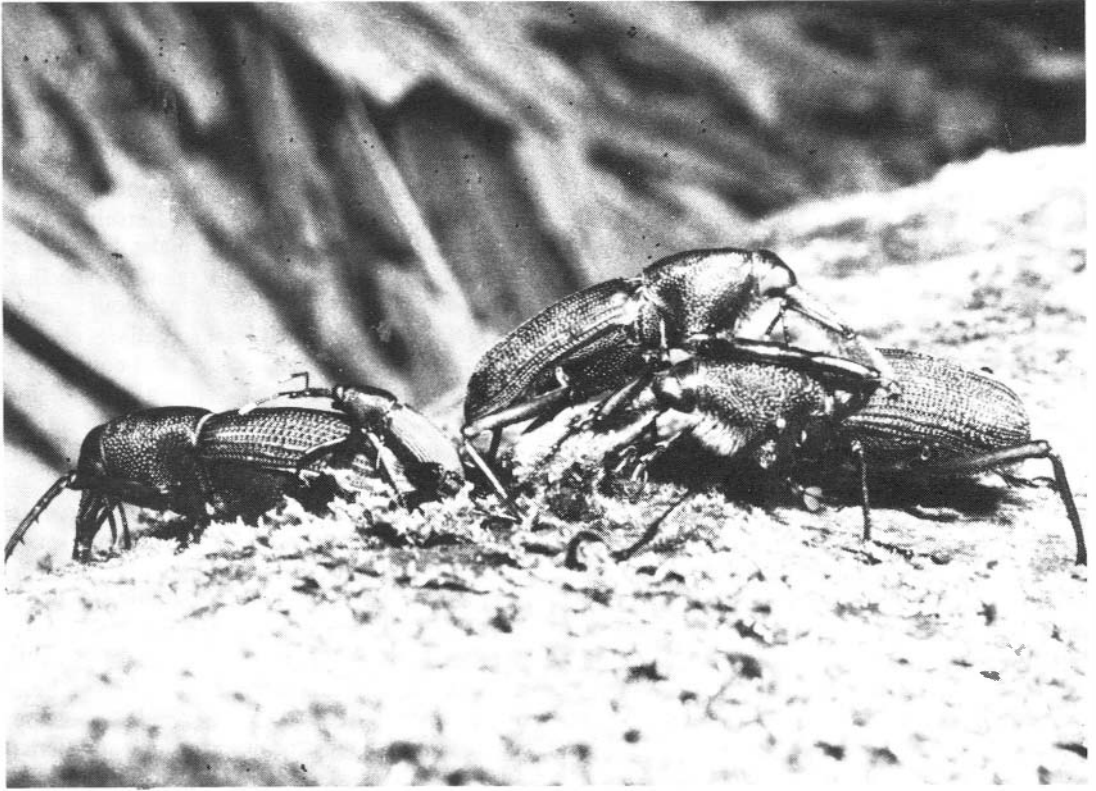


Fig. 7. Three males battle over a drilling female. While the two large males attempt to knock each other from the log, a dwarf male copulates with the female after approaching surreptitiously.

scattered along the trunk, with the male periodically wiping the dorsum of the female with his rostrum as she drills or walks slowly along the surface. One or two unaccompanied females are also more or less motionless as they inspect recently laid eggs or rest. Five to ten males make up the rest of the population, and they scurry restlessly back and forth along the trunk, searching for females. Brief clashes break out frequently between searching and attendant males, with the larger individuals usually winning. When an attendant is displaced, the winner stays with the female and wipes her and copulates with her, while the loser rejoins the hectic rush of solitary males.

DISCUSSION

Probable explanations of several striking behaviors of the males—their frenetic activity, their extreme aggressiveness toward other males near females and disinterest away from them, their general failure to stay with females

once an egg is laid, and their elongate front legs and rostra— seem to hinge on 1) the probability of sperm precedence in the female's spermatheca— whether it is the most recently deposited sperm which is used by a female to fertilize a given egg, and 2) rapid movement of sperm into the spermatheca after mating. Sperm precedence of this sort is known in the only species of weevil (*Anthonomus grandis*) which has been studied from this point of view (Bartlett *et al.*, 1968), and may be typical of Coleoptera (Walker, 1980). Krautwig (1930 in Khan and Musgrave, 1969) noted that the aedeagus of the weevil *Sitophilus* probably reaches to where the spermathecal duct opens into the bursa copulatrix— close to the site where fertilization presumably occurs. Villavaso (1975) also found that after *A. grandis* mated sperm were present in the bursa and were capable of fertilizing eggs. Thus a male *R. barbirostris* probably reproduces most effectively by copulating almost immediately with every newly encountered female, and then fighting

to keep other males from supplanting him, thus keeping his own sperm in their privileged position until the female lays her egg. One can reason that a single copulation probably results in deposition of sufficient sperm to fertilize at least two eggs since males accompanying females after a first oviposition did not attempt to remount and copulate a second time; in addition a female dissected just after she had oviposited had abundant, active sperm in her spermatheca.

As soon as the egg has been fertilized (judging by the males' behavior, soon after the female turns to begin oviposition), the male is faced with the options of either A) staying with this female and attempting to defend her until her next oviposition, or B) leaving her and searching for another female that is nearly ready to oviposit. The high concentrations of individuals on the logs and the relatively long times between successive ovipositions by given females could both decrease the adaptiveness of option B with respect to A since they would make it more difficult to defend the female successfully until the next oviposition and at the same time increase the chances of finding another female. The very individuals (larger males) for which option A would be most likely to yield results (they would be relatively certain of being able to successfully defend the female until the next oviposition) would also be the same ones most likely to benefit from option B since they would be most likely to be able to take over possession of females ready to oviposit. The result is the usual choice of option B, and the aggressive "rat race" behavior of the males, since both females and the time to find them are at a premium.

Two of the secondary sexual characters of males —elongated rostra and front legs— probably function as weapons in aggressive interactions between males and are thus in accord with the tendency for exaggerated features of male morphology in other beetle species to function as weapons (Eberhard, 1977; Palmer, 1978; Eberhard, 1979 and references; Eberhard 1980). A male with a longer rostrum can raise an opponent higher with a flipping movement, and thus has a better chance of dislodging him from the log. A longer rostrum also increases a male's range and permits him to hit opponents at greater distances. Long legs enable a male to raise the anterior part of his body far off the trunk (Fig. 6). and thus to both deliver a

higher and more effective flip to an opponent and also to absorb a stronger flip without being knocked off himself.

The morphological specializations for aggressive interactions are paralleled by the beetles' pugnacious dispositions which occasionally took them to the apparently nonadaptive extremes of continuing to fight fiercely in the litter under a log after both males had fallen from the neighborhood of a female. Even this level of ferocity may be advantageous, however, since males were at least sometimes clearly intimidated after being beaten, and continuing a still unresolved fight with a potentially beatable opponent could function to make subsequent encounters with this individual easier to win.

Another unusual feature of *Rhinostomus* are the mandibles, which appear in both sexes to be designed to cut with their outer rather than inner surfaces (Vaurie 1970). Kissinger (in Vaurie 1970) commented that they may "...function by cutting or ripping through fibrous material essentially to punch a hole for oviposition... when the mandibles are opened, either they may rip through additional fibers enlarging the hole... or the resistance of the fibers may enable the mandibles to shove the tip of the beak down, something like a breast stroke..." The fact that small chips of wood accumulated around the edges of oviposition holes as they were drilled seems to rule out the "breast stroke" mode of operation, and also suggests that more than simple cutting or pushing aside of fibers is occurring. Indeed the palm trunks were very hard, and real drilling was clearly necessary to bore holes. The way females used their rostra as they finished holes suggested that at least at that stage the outer rather than the inner surfaces of the mandibles were being brought to bear on the wood.

The functional significance of one other secondary sexual character — the thick brush of hair on the rostrum and (in larger males) the ventral surface of the prothorax — is still not clear. The wiping behavior of attendant males brought this hair into direct contact with the female, and as noted, the males modulated the intensity of wiping behavior as if it somehow induced the female not to move away, and males even sometimes "wiped" dwarf males (evidently mistaken for females?) into immobility. A related possibility is that the hairs

stimulate the female to allow intromission and are thus under sexual selection by female choice. The greater hairiness of larger males (compare Figs. 4 and 7) could thus represent a display character which the female presumably senses as he wipes her dorsal surface. These ideas, although attractive, fail to explain the presence of hairs (less dense but still present in substantial numbers) on the *dorsal* surface as well as the ventral surface of the rostrum, since the dorsal surface never made contact with females during wiping behavior. Another possible function is that the hairs are sensory organs used by the male to sense some stimulus from the female. The behavior of patrolling males when they encounter other beetles argues that the hairs are not to recognize the sex of other individuals, but they might sense other cues from females (e. g. reproductive state). A final idea is that they serve to prevent or promote slippage when strong forces are applied by the rostrum. This seems not to be the case in *R. barbirostris* however since it is only the more sparsely hirsute dorsal surface which strikes opponents; probably the knobiness of the cuticle of this surface serves to reduce slippage. The male of the weevil *Sitophilus granarius* also rubs his beak on the dorsum of the female (Wojcik, 1969), but lacks a brush of hair.

It is suggestive that males of some other beetles whose behavior has been studied (e. g. the scarabs *Podischnus agenor* and *Golofa porteri* [Eberhard 1977; 1979] and the tenebrionid *Bolitotherus cornutus* (Pace 1967, pers. comm.) also have dense mats of hair on body parts (thoracic horns, tarsi) which are brought into direct contact with conspecifics. In none of these species is there any behavior comparable to the wiping of *R. barbirostris*. It is also interesting that other *Rhinostomus* species have long hairy front legs (Vaurie, 1970). Perhaps the mats of hairs have multiple functions, even within the single species *R. barbirostris*.

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RESUMEN

La historia natural del abejón picudo barbado *Rhinostomus barbirostris* fue observado en el occidente de Colombia donde las larvas minan troncos caídos de palmas, y concuerda con las descripciones previas de regiones en donde esta especie es una plaga del coco. Se determinó que algunas de las características secundarias sexuales de los machos adultos (pico más largo, patas primeras más largas, y mayor actividad y agresividad) sirven en las peleas que se desencadenan entre machos alrededor de hembras que están perforando al tronco para ovipositar. Otra característica (la densa pilosidad sobre el pico y en la superficie ventro-anterior del torax del macho) puede servir como parte del cortejo del macho, pero esta explicación no es completamente convincente.

Existe una gran variedad de tamaños entre los adultos, aparentemente por diferencias en el sustrato donde minan las larvas. Los machos grandes casi siempre ganan a los más pequeños en peleas abiertas. Estos últimos emplean dos tipos de comportamiento especial que parece ser diseñado para compensar en algo esta inferioridad como peleadores. Así es posible que los machos sean polimórficos en cuanto a su comportamiento agresivo, pero no hubo señal de un polimorfismo en cuanto a las armas morfológicas, ya que la relación largo del pico-tamaño del cuerpo fue estrictamente lineal. El comportamiento de los machos sugiere que en esta especie la hembra tiende a utilizar los espermatozoides del último macho con el cual haya copulado para fecundar cada huevo que pone.

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