

RITUAL JOUSTING BY HORNED *PARISOSCHOENUS EXPOSITUS* WEEVILS (COLEOPTERA, CURCULIONIDAE, BARIDINAE)

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ABSTRACT

Males of the weevil *Parisoschoenus expositus* use their prothoracic horns as weapons in stylized battles with other males over females that are drilling oviposition holes in palm leaves. The unusual sheath-like structures that penetrate deep into the male prothorax function to receive the horns of opponents during battles. Horn size is dimorphic with respect to body size, and small and large males also differ behaviorally. Small males that have mated with a drilling female are sometimes able to impede a large male's access to the female until after she has oviposited, but they are not able to take over females from larger males.

INTRODUCTION

Beetle horns are extremely diverse in size and shape (e.g., Arrow 1951; Eberhard 1979). Despite occasional claims to the contrary (Møller 1992), observations of their use in natural contexts suggest that they function as weapons in battles between conspecifics (Morón 1976; Bechtle 1977; Eberhard 1977, 1979, 1981, 1987; Palmer 1978; Brown and Siegfried 1983; Otronen 1988; Connor 1988; Siva-Jothy 1989; Rasmussen 1994; Emlen 1994, 1997), rather than as visual display devices as do the horns and antlers of some ungulates (Geist 1966, 1978; Lincoln 1994). Three common functional designs have been documented among beetle horns: a dorso-ventrally mobile head horn which serves as a lever to lift the opponent and (in some species) to

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clamp him against an immobile prothoracic horn or horns [Beebe (1944, 1947), Morón (1976), Eberhard (1977, 1979, 1987), Palmer (1978), Otronen (1988), Siva-Jothy (1989) on scarabeids; Eberhard (1979) on ciids]; elongations of the mandibles that can be opened and closed to clamp the opponent [Goldsmith (1987) on a cerambycid; Bechtle (1977) and Hamilton (1979) on lucanids; Eberhard (1979) on a tenebrionid]; and immobile, more or less straight horns that project anteriorly or posteriorly and are used as levers to pry opponents from the female or from the substrate [Brown and Siegfried (1983); Brown and Bartalon (1986); and A. Pace (personal communication) on a tenebrionid; Eberhard (1981) on a chrysomelid; and E. Sleeper (personal communication) on a brentid]. In many species the winning male physically removes the loser from the vicinity of the female (i.e., tosses him to the ground), or blocks his access to her (i.e., pushes him from the tunnel leading to her and defends against reentry).

Apparently the only armed weevils whose behavior has been carefully studied to date do not have horns. Males of *Rhinostomus barbirostris* use their thick, elongate rostrum and their long front legs to pry other males and flip them from logs where females are ovipositing (Eberhard 1983); and males of *Macromerus bicinctus* use their swollen front tibiae and elongate front legs as clubs to strike opponents in threat displays (Wcislo and Eberhard 1989). Fragmentary observations of the horned *Centrinaspis* sp. indicated that males apparently push each other (Eberhard and Gutierrez 1991; W. Eberhard, unpublished), but the possible role of their horns was not determined. The only other published observation of which we are aware concerning possible use of prothoracic horns or spines in a weevil is that of Lyal (1986) of a single encounter between males of the zygotine genus *Mecopus*, in which "the thoracic spines did not appear to be employed, although the movements were so rapid that precise observations were not possible."

There are many other types of horns whose mechanical designs suggest that they are not used in any of the ways documented for other beetles, and whose functional significance thus remains unknown. This study concerns one such design in the small (approximately 2 mm long) baridine weevil *Parisoschoenus expositus* (Champion 1908). Males of *P. expositus* have a pair of horns or spines projecting anteriorly from the prothorax, and a deep invagination in the anterior surface of the prothorax between the bases of the horns. Large males have

horns that project to the rostrum, while very small males completely lack horns (Fig. 2).

METHODS

Collections and behavioral observations were made during the day near Parrita, Puntarenas Province, Costa Rica (elevation about 20 m) on 19-30 January 1998, in a plantation of approximately 8 m tall African oil palms (*Elaeis guianensis*). Beetles were observed on the cut petioles of the large (several meters long) leaves which had recently been trimmed from the trees and whose pinnae were still green. Most observations of behavior were made using a 2X headband magnifier and a 10X hand lens (working distance 2 cm). The combined magnification allowed detailed observations, and confident field evaluations of approximate male horn size without collecting and measuring beetles (large horns were about 0.3 mm or more; short horns were less than about 0.3 mm). Approximately two hours of behavior was videotaped, using a Sony CCD-TR700 camcorder with +7 close-up lenses. All drawings illustrating behavior were traced from video images. Those portions of the animals' bodies that were not clear in the videos were omitted in the drawings.

Possible differences in colonization behavior were checked by making fresh cuts with a machete near the bases of trimmed leaves and setting them out in the same piles of trimmed leaves. Beetles were collected both on the surfaces of cuts, in the cracks that formed when the rachis dried, cracks where the leaf had been split when it was cut, and the narrow spaces between the matted tissue and fungus that were generally present on what had been the ventral surface of the leaf. Collections of beetles on open surfaces and in cracks were made around midday (10:00-13:00 hrs) on leaves which had been on the ground for at least 4-6 days.

Beetles were measured using an ocular micrometer to the nearest 0.025 mm. Each specimen was aligned for measurement in lateral view (Fig. 1) by adjusting its position until the tip of one horn lay just over the tip of the other horn. The lateral curvature of horns was estimated by positioning the beetle's ventral surface upward so that the bases of the horns and their tips were all in focus at once, and then measuring the distances between the bases of the horns, between their tips, and between their midpoints.

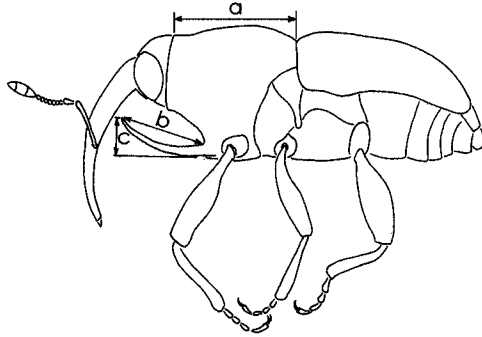


Fig. 1. Measurements made on specimens: (a) prothorax length; (b) horn length; (c) dorsal curve of horn.

Measurement precision was tested by remeasuring beetles on different days. The average difference between repeated measurements of the prothorax length of 51 specimens was 0.0083 ± 0.0138 mm, or about 0.8% of the average prothoracic length; respective values for remeasurements of the horns of 17 specimens were 0.0088 ± 0.015 mm or 2.2%. Averages are given followed by \pm one standard deviation. Estimates of the densities of setae on horns were calculated from SEM images assuming the horn was a cylinder and that half of the horn's surface was visible in lateral views.

Specimens to be examined with the SEM (S-2360N) were dehydrated from glutaraldehyde and Karnovsky solution, dried by sublimation, and coated with $20 \mu\text{m}$ of gold. Voucher specimens have been deposited in The Canadian Museum of Nature (Ottawa), The Museum of Natural History (London), the U. S. National Museum (Washington, D. C.), and the Museo de Insectos of the Universidad de Costa Rica.

RESULTS

A. Morphology

All but the very smallest males of *Parisoschoenus expositus* had a pair of rigid, pointed horns (or spines) projecting anteriorly from the ventral portion of the anterior surface of the prothorax (Fig. 2). The shapes of these horns varied substantially with male size. In small males the horns were small nubbins (Fig. 2) or were entirely lacking. The horns of medium-sized males were nearly perfectly straight, and each was directed anteriorly and somewhat laterally (Figs. 2, 3). The horns of large males curved both laterally and dorsally. The surface of horns of all sizes was smooth and relatively free of the setae that covered most other body surfaces (Fig. 2). Horns bore only scattered, short setae, each set in a small pit (Figs. 2, 4). In two large males carefully examined in the SEM the density of these setae was greater near the base of the horn (about 2375 $\mu\text{m}^2/\text{seta}$) than near the tip (about 4300 $\mu\text{m}^2/\text{seta}$).

Larger beetles had larger horns (Fig. 5), and a statistical analysis of all males except those completely lacking horns similar to that of Eberhard and Gutierrez (1991) (but using untransformed data, since transformations did not improve fits) revealed that there were two different body plans (both deviation from linearity and the test for a switch point were significant, $p < 0.01$). The percent of the explained variance in horn length increased from 74% with a single regression line to 85% with a two part regression, using the break point of horn length of 0.42 mm (Fig. 5). The distribution of horn lengths was flatter than that of prothorax lengths (Fig. 5). The distribution of female prothorax lengths was very similar in shape to that of the males.

The horns of large males were more curved dorsally and laterally than those of small males, but the patterns of difference were not the same. Males with horns less than about 0.30 mm had no dorsal curvature, and from this size upward the amount of curvature increased steadily with greater horn length (Fig. 6a). In contrast, even in males with short horns the horns projected laterally, and the amount of lateral curvature increased with horn size until the horns were about 0.5 mm and then leveled off (Fig. 6b).

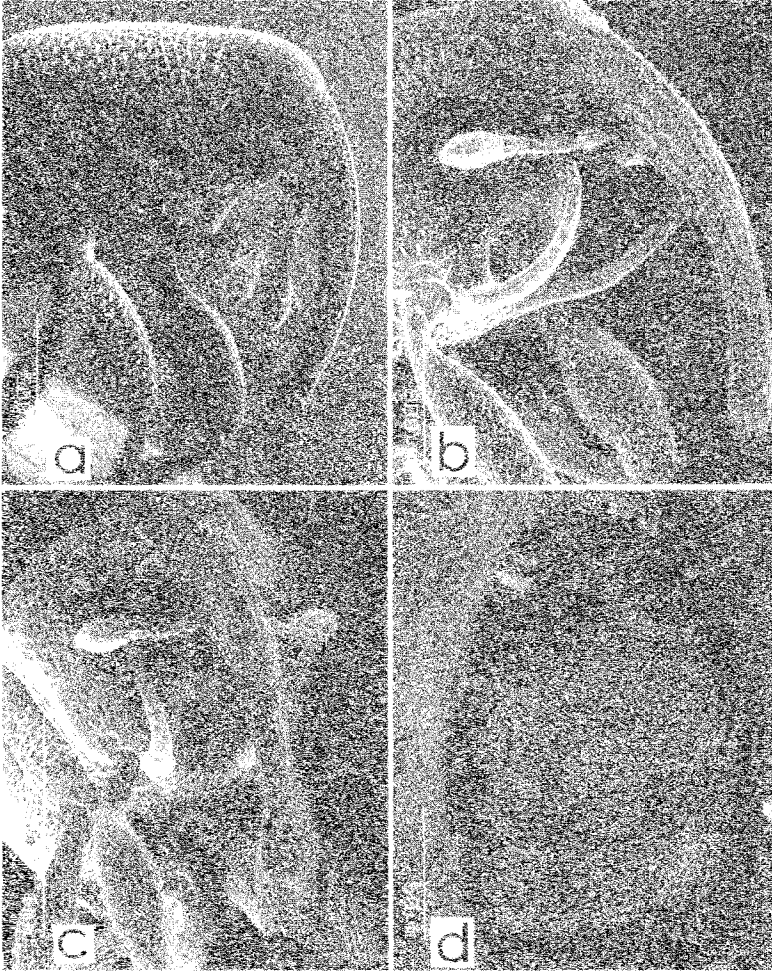


Fig. 2. Horns and pits of males: (a) small male with short straight horns and only a hint of a pit between them; (b) large male with long curved horns and a pit between their bases; (c) anterior view of the opening of the pit of the large male, showing its beveled edges and the low density of setae; (d) close-up view of the inner surface of the pit.

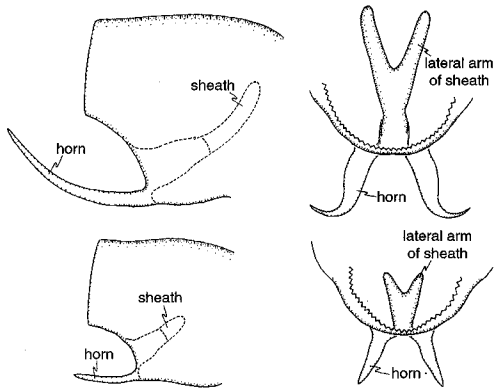


Fig. 3. Lateral and dorsal views of the horns and prothoracic sheaths of a large (above) and a medium-sized male (below) (drawings of sheaths were made by dissecting away the prothoracic wall).

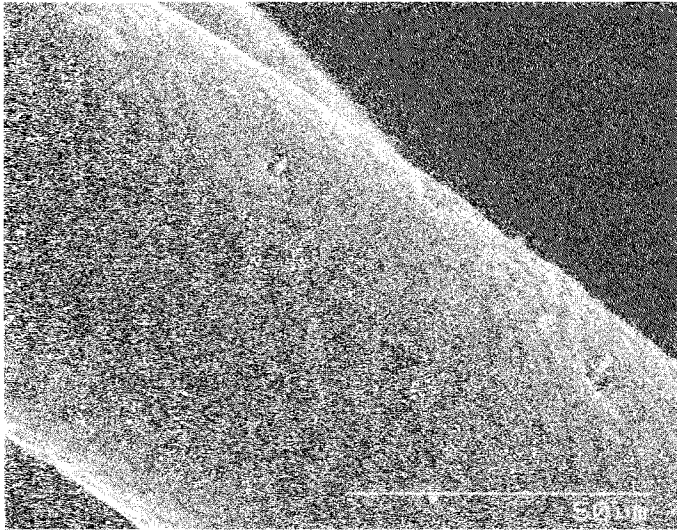


Fig. 4. Short, presumably sensory setae in small pits on the surface of the horn of a large male.

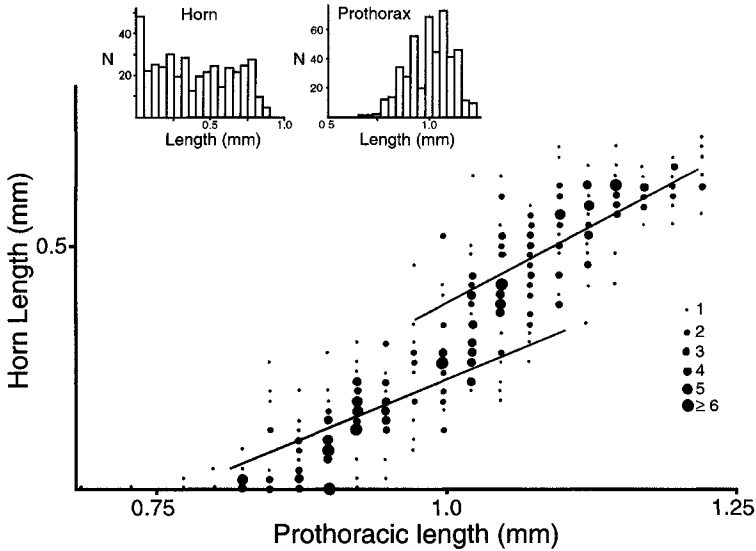


Fig. 5. Relationship between prothorax length and horn length of males. The insets show the frequency distributions of prothorax and horn measurements.

The surface of the prothorax of moderate and large-sized males was deeply invaginated, forming an oval pit between the bases of the horns (Figs. 2b-d). The surrounding surface had few setae and sloped toward the pit (Figs. 2b, c). Internally the pit led to a short central tube whose internal walls were also relatively smooth and lacked setae (Fig. 2d). This tube extended posteriorly and dorsally, and branched to form a pair of long, relatively straight, blunt-ended tubular arms which extended deep into the prothorax (Fig. 3). The internal diameter of each sheath was substantially greater than the diameter of the same male's horns (Fig. 3). The cuticle of each sheath was strong and inflexible. The branches of the sheath were straight, even in large males whose horns curved strongly (Fig. 3).

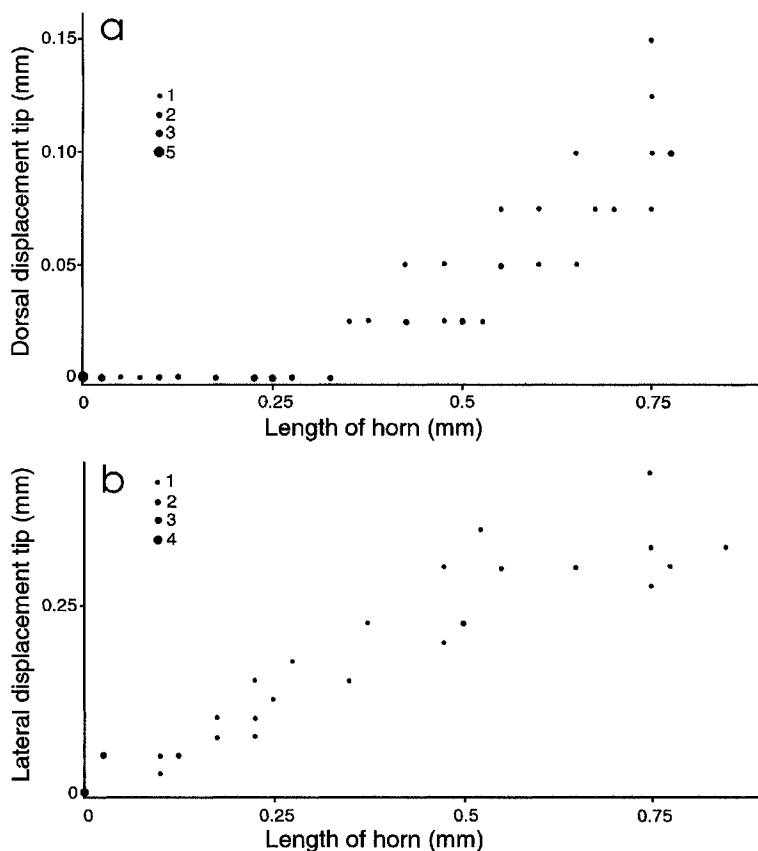


Fig. 6. Relationships between amount of dorsal (a) and lateral (b) curvature of horns and horn length.

The functional significance of the sheaths was revealed by placing males in positions similar to those seen during horn locking fights in nature. The near-side horn of each male entered the opposite-side sheath of the other male, occupying approximately half the inner diameter of the sheath (Fig. 7). Thus, when the right horn of male A entered the left sheath of male B, the right horn of male B entered the left sheath of male A. Because of the rigidity of the horns and sheaths, it was impossible to insert one male's horn into another similarly horned opponent unless the opponent's horn was simultaneously inserted into the first male's sheath. In two pairs of specimens that were manipu-

lated into horn-locking positions (one pair of large males, the other of medium-sized males), the angle between the dorso-ventral axes of the two males measured, respectively, 71° and 73° . Thus in nature each male must have to tilt about 36° laterally away from an opponent to engage him in a horn-locking battle.

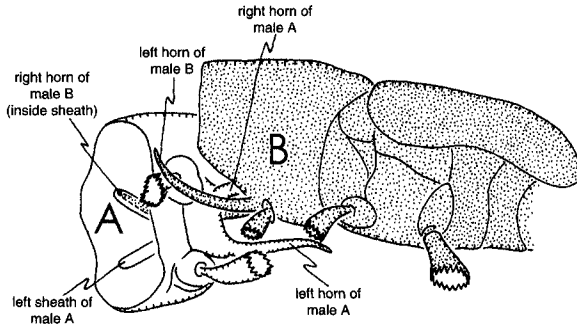


Fig. 7. Horn-locking positions of two partially disarticulated large males. The right horn of male B (stippled) is lodged deep in the right sheath of male A.

B. Behavior

Beetles occurred on both fallen trimmed leaves and the cut leaf stub remaining on the tree. Beetles that had wedged themselves into cracks on or near the cut surface (and into folds of plastic bags where some were kept temporarily) were immobile. This immobility and the lack of space in which they could execute the maneuvers associated with mating, fighting and oviposition suggest that their sexual behavior does not occur in cracks. Beetles found during the morning on less recently cut leaves, whose pinnae were still green but beginning to brown, were all in cracks. No beetles were found on leaves whose rachis was still green but whose pinnae had all turned brown.

1. Oviposition

Drilling and oviposition were preceded by apparent searching behavior. The female walked slowly over the cut surface of the leaf, repeatedly touching it with the tip of her rostrum and her antennae. She often paused with the tip of her rostrum touching the palm for variable amounts of time that lasted up to several minutes. It was not clear whether these pauses represented feeding or searching for oviposition

sites. Of a total of 22 females that were followed after an oviposition, 9 eventually laid a second egg, 9 walked into a crack or off the cut surface, and 4 more were lost from view (probably also went off the cut surface). None of these females laid a third egg while being followed. The time between ovipositions ranged from 2 to 43 min. (mean 19.3 min.).

Oviposition was always preceded by a period of "drilling," during which the female ceased walking and inserted her rostrum into the leaf (e.g., Fig. 9). The shortest drilling was just under 2 min., while the longest was over 6 min. The female sometimes inserted her rostrum all the way to her eyes. In at least one case a female made a deep hole, but then abandoned it without ovipositing. It is possible that some "drilling" was actually feeding behavior. There were few if any perceptible prying or turning movements during drilling, such as were performed by drilling *Metamasius* sp. females on the same palm leaves. Nor did drilling females bring pieces of plant tissue ("sawdust") to the surface or work at the edge of the hole just before oviposition, as do those of *Rhinostomus barbirostris* (Eberhard 1983). The end of drilling was marked by a smooth withdrawal of the rostrum and a 180° turn. As will become clear, the lack of overt signs that distinguish female searching or feeding behavior from drilling and impending oviposition has important consequences for understanding male behavior.

When the female turned 180° after drilling, she positioned the tip of her abdomen at the mouth of the hole left by her rostrum, sometimes after brief searching behavior with the tip. The tip of her abdomen was extended, and she remained immobile for an average of 35 ± 10 seconds ($N = 24$). She then immediately turned 180° and "worked" on the material where oviposition had occurred with the tip of her rostrum for an average of 72 ± 12 seconds ($N = 5$). Both her antennae repeatedly touched the surface of the palm near the tip of her rostrum, and the tip of the rostrum appeared to pull together and gently tamp down material on the surface.

2. Courtship

The male mounted the female with no preliminary courtship, and positioned himself to face in the same direction. Females were almost never mounted if they were walking. After a variable amount of time (ranging from <10 seconds to 166 seconds in 18 pairs), the male performed courtship behavior and then attempted intromission. The first

behavior pattern (omitted in some pairs that nevertheless copulated) was to briskly rub the tip of his rostrum back and forth across the surface of the female's pronotum. The exact direction of these rubs varied, but was often largely from side to side. Very small males mounted on large females rubbed the female's elytra rather than her pronotum.

Following rostrum rubbing, the male moved posteriorly on the female to position the tip of his abdomen near the tip of hers, and vigorously rubbed the lateral and ventral surfaces of the posterior portion of her abdomen with the ventral surfaces of his folded hind tibiae (Fig. 8a). Tibial rubbing occurred in bursts of approximately a second, and was either accompanied or immediately followed by partial eversion of the male's genitalic basal lobe and one or a series of small, rapid stabbing movements with it against the tip of the female's abdomen. Intromission occurred at this stage if the female was receptive and opened the tip of her abdomen. Rubbing was sometimes reduced to as little as a single rub, and sometimes omitted entirely. If

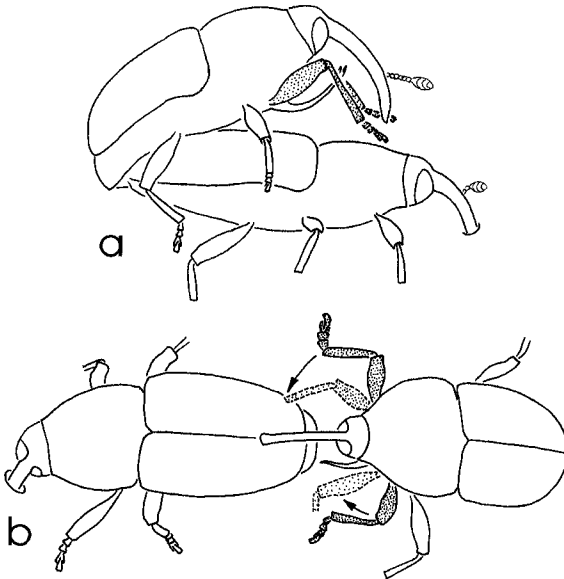


Fig. 8. Patting behavior: (a) a male raises both front legs (stippled) preparatory to patting the female during copulation; (b) a partially dismounted male pats the female soon after copulation ended (dotted lines followed others by 0.1 second).

intromission was not successful, the male either rubbed again with his hind tibiae and tried to intromit again (often successfully), or moved forward again. The maximum number of intromission failures was three, and most males were successful on their first or second intromission attempts. One male that had just failed to intromit moved forward, vibrated his entire body briefly (see description of stridulation in the section on aggression below), and moved back to rub with the hind tibiae and attempt intromission again. In no case was there any sign of female attempts to dislodge males by kicking or other body movements. Nor was there any sign of contact with or other display of the male's horns.

3. Copulation and after

Copulation lasted an average of 100 ± 46 seconds ($N = 29$). The male was usually immobile during most of copulation, except for a steady pumping movement of the tip of the male abdomen [Fig. 9a; see Eberhard (1994) for a verbal description of very similar movements in seven other species of curculionids]. When another beetle passed nearby, however, the male usually vibrated his head rapidly dorso-ventrally (Fig. 9b). This movement appeared to be designed to produce sound by rubbing the head against the anterior edge of the prothorax, but there were no stridulatory structures on the head or prothorax, and female morphology in this region was similar to that of males. Head movements may instead function as visual signals. Two males rubbed the female's pronotum briefly during copulation with the rostrum as in pre-copulatory courtship behavior. In 5 of 13 carefully observed pairs, the male became active during the last approximately 5-15 seconds of copulation, patting the female rapidly on the pronotum with one or both of his front legs (probably contacting her with the tips of his tibiae and tarsi; see Fig. 8b).

The male ended copulation by withdrawing his genitalia and stepping posteriorly, often dismounting to stand just behind the female with his head and at least part of his prothorax over her elytra. Usually (16 of 19 cases checked for this detail) the male patted the female's dorsal surface with one or both front legs in one or several shorts bursts of movement after dismounting (Fig. 8b). In the most elaborate form of these post-copulatory displays the male stood with both front legs raised and partially extended anteriorly, and then delivered several bursts of rapid simultaneous pats with both front legs. Each pat lasted

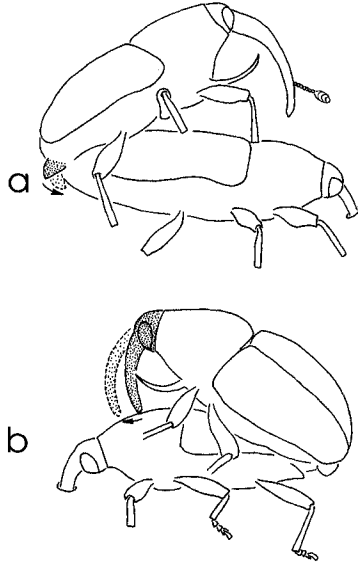


Fig. 9. Movements of the male during copulation: (a) pumping movement of the tip of the male's abdomen during copulation (dotted lines follow others by 0.1 second); (b) a large male vibrates his head dorso-ventrally while copulating with a drilling female (dotted lines follow solid by 0.07 second).

about 0.03 second, and bursts of pats lasted up to a second or so. As in pre-copulatory courtship, the male horns were never in positions that would allow them to stimulate the female tactilely; nor was the male positioned appropriately to emphasize their visual impact on the female.

A drilling female often copulated with several males, and the final copulation frequently ended only shortly before oviposition. In 22 pairs, oviposition followed the end of copulation by <30 seconds in 8, and by <60 seconds in 14. Male defense of the female (next section) usually ended abruptly as soon as the female turned to oviposit. In 14 of 24 carefully timed pairs the male left within 10 seconds after the female turned (in some pairs he departed less than 1 second after she turned). In only 1 of the 24 was the defending male still near the female 60 seconds after oviposition began. Of 58 cases in which the initiation of oviposition was observed, the last male to accompany the female was judged to be large-horned in 48 (in 31 of these cases copu-

lation by this male had been observed); and in 9 the last male was judged to be small-horned (in all 9 pairs copulation by this male had been observed) (the other case involved a male whose horns were intermediate in length).

Females never showed any resistance, such as walking, kicking, or shaking their bodies, to being mounted or ridden by a male. Many mounts, however, did not result in copulation attempts because the male dismounted immediately and moved away if the female was not drilling, especially when she began to walk (in 12 of 15 cases checked for this detail). Thus a female in the process of searching for an oviposition site was generally mounted briefly but then abandoned by a series of different males (and sometimes repeatedly by the same male). The longest such fruitless mount, which involved a female that was not walking, lasted 10-11 min.

A second common type of fruitless mount was while the female was motionless during oviposition, during tamping behavior following oviposition, or when her abdomen protruded while she was motionless with her anterior end inserted into a small crack. Males almost always abandoned such females immediately, however, as soon as they began to walk.

4. Aggression

Females never interacted aggressively with each other, except in a single case in which one female attempted to push her rostrum under that of another which was drilling. In contrast, male-male aggression was very common. After a male copulated with a drilling female, he always remained with her and attempted to defend her against other males. Aggressive behavior in defense of the female took several forms that will be described in order of increasing intensity. Usually a male's first defensive response to another beetle approaching from in front of the female was to move forward onto the female and vibrate his head dorso-ventrally (Fig. 9b) and make patting movements with his front legs. Patting in this context amounted to hitting movements directed toward the other beetle that fell short. If another beetle approached from the side or the rear, the male leaned toward the intruder, thus interposing his body between the other beetle and the female. Sometimes this maneuver succeeded in keeping the other male (even a larger one) from encountering the female, and he walked on without further interaction. In nearly all cases in which a large male

defended a female against a small male in this way, the small male simply walked away. In all nine cases in which a large male approached a small male while he was copulating, the small male broke off copulation to interpose his body between the female and the other male. In contrast, large males did not break off copulation when small males approached (17 cases), but only vibrated their heads vigorously, and the small male left without further interaction.

If the defending male was particularly small with respect to the invader, the defender sometimes crouched down immobile alongside the female against the surface of the leaf. This behavior was seen on eight occasions. The large male usually tried to dislodge the small male, often by prying him with his rostrum, but in one case he apparently failed to notice the small male, which was later able to attempt to mate with the female while the large male was battling another male. In no case did a large male use his horns to pry or lift a crouching male (as, for instance, elephants use their tusks to move logs).

When an invading male was not deterred by low level defensive behavior, a more serious battle resulted. These battles had two different forms. In lower apparent intensity, the two males faced each other as their legs and rostra entangled and each male repeatedly pushed forward. Often one or the other vibrated his abdomen rapidly dorso-ventrally. This behavior probably resulted in stridulation, as males had typical curculionid elytral file and tergal plectrum structures (Fig. 10; see Lyal and King 1996). Most pushing battles involved repeated changes of position, and it was not always easy to determine what each male was attempting to accomplish. In some fights in which one male was substantially larger than the other (and could thus presumably do more or less what he wished), the larger male pushed the smaller one several body lengths from the female, repeatedly turning him partially onto his back as he did so. Although males were capable of opening their mandibles wide enough to grasp portions of the opponent's body such as his antennae (Fig. 11), and although in many fights the tip of a male's rostrum contacted his opponent, there were no signs that males bit each other (i.e., we never saw one male pull away with the other's mouthparts holding his leg or antenna).

The horns did not appear to play important roles in these battles. It was clear that the horns were never used in conjunction with the rostrum to clamp and raise the other's body (such a use might be expected in view of how other beetle horns are used; see the Introduction).

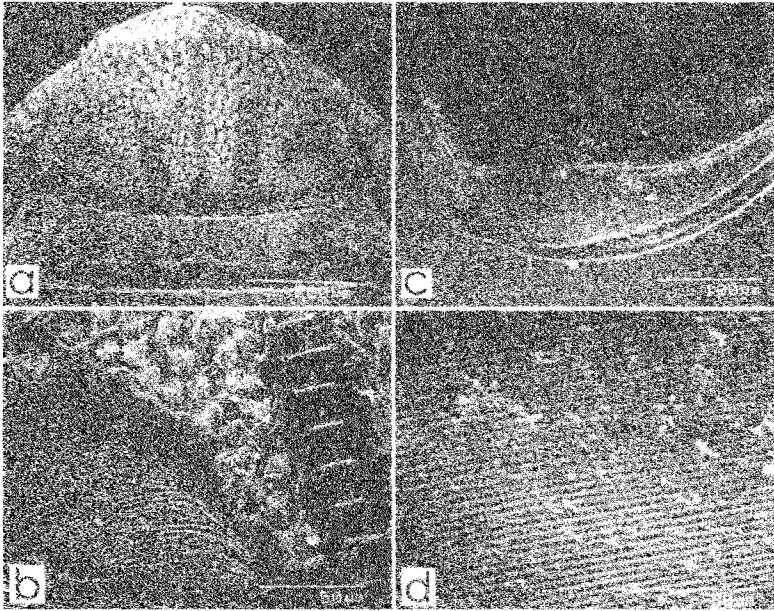


Fig. 10. The abdomen-elytrum stridulating organ: (a) dorsal view of the plectra on the anterior dorsal surface of the pygidium, each of which consists of several linear ridges bearing a single strong blunt spine; (b) close-up of ridges and spines; (c) finely striated file on the posterior edge of the left elytrum; (d) close-up of the file.

Details of movements during fights suggested that a male's most important offensive behavior was pushing and prying with his rostrum rather than with his horns. Males consistently lowered rather than raised their heads, and inserted their rostra under their opponent's bodies during apparent attempts to lift and push (e.g., Fig. 12a). They did not raise the rostrum and then insert the horns under the opponent, as would have been expected if the horns function as levers. The rostrum sometimes pressed sideways on the opponent, or swept forcefully sideways in an apparent attempt to move him (Fig. 12b). In some taped fights a male's rostrum briefly flicked dorsally. Similar quick lifting movements of the entire anterior portion of the male's body, which would be expected if the horns were used as levers, seldom occurred; in at least some cases when a lifting movement did occur, the dorsal surfaces of the male's head and rostrum rather than his horns were in contact with the ventral surface of his opponent.

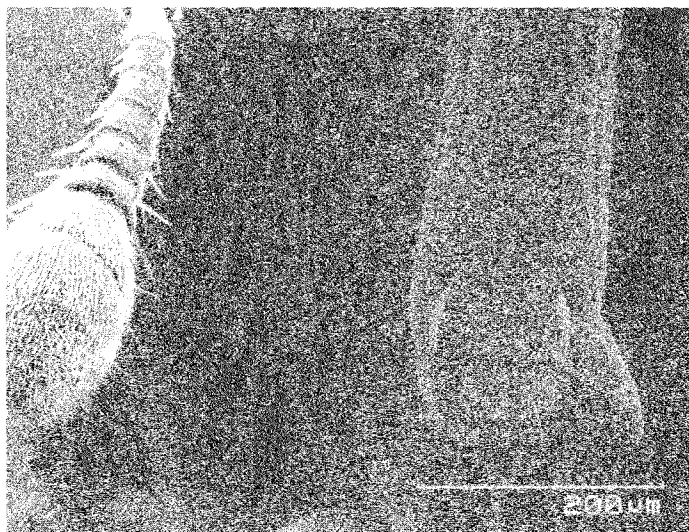


Fig. 11. Mouthparts and antenna of a large male, showing that the mandibles can open wide enough to seize the antennae.

Another movement, which was too rapid to be seen easily with the naked eye but that occurred repeatedly in video recordings, was to slap the opponent forcefully with one front leg. Slapping occurred as rapidly as 4 times in the space of 0.97 second with the same leg, and was very common in some fights. For instance, one taped pair slapped each other at least 10 times in 3.5 seconds; another male that came on a pair of fighting males slapped at least 14 times in 4.5 seconds.

The highest intensity battles involved males locking horns. Preparatory to a horn-locking battle each male crouched slightly toward the substrate, tilted his body to the side away from the other male (presumably approximately 35° to the side; see above and Fig. 7). Then each male pressed his prothorax straight ahead against the prothorax of the other, and their antero-lateral surfaces became tightly apposed (Fig. 13). It was clear that horn-locking could only occur if both beetles aligned themselves in this manner. In some pairs, one male (usually the larger) appeared to assume the locking posture repeatedly, but locking did not occur because the other male did not align himself in the same manner. Nearly all horn-locking battles involved relatively large males, but in one case two small males (which had come upon a drilling

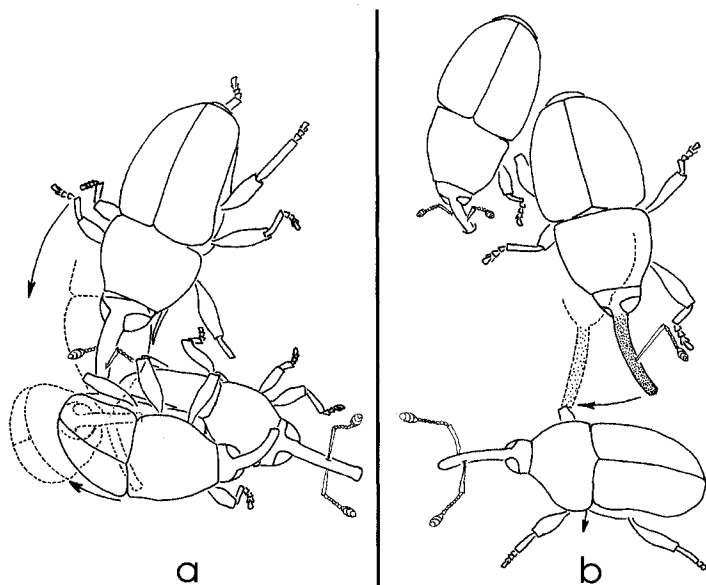


Fig. 12. Using the rostrum to pry and hit in fights. (a) The large male (top) lunges forward (dotted lines follow the others by 0.63 second), prying the mounted male posteriorly and away from the female. Note that the large male's horns did not make contact with his opponent prior to the push. (b) A large male, which has moved away from a drilling female and toward a passing male, slaps laterally with his rostrum (dotted lines follow others by 0.07 second) and hits one of his opponent's legs. The other male immediately pulled away (displacement in next 0.07 second indicated by arrow).

female while two other large males fought for her nearby) fought briefly in what appeared to be a horn-locking battle; another horn-locking fight involved two evenly matched medium-sized males.

Once the two males had pressed together, their positions relative to each other scarcely changed during the rest of the battle. Each male's head was alongside the meso- and metapleura of the other male, with the tip of his rostrum just short of the opponent's hind coxa (Fig. 13). Usually both males actively vibrated both their heads and their abdomens dorso-ventrally, presumably rubbing the opponent (with the head) and stridulating (with the abdomen). During some horn locking fights a male's entire body seemed to shudder; it was not clear whether this involved a distinct movement, or was simply a violent vibration of the abdomen.

Once a pair of males locked horns, they usually appeared to push each other repeatedly. Judging by the sudden movements of some pairs, some pushes were quite forceful. In no case, however, did the males move more than a few steps in any direction. The duration of horn-locking fights varied from <5 up to 140 seconds ($N = 21$). In longer fights there were often periods during which the beetles stridulated but did not move otherwise (either they ceased pushing, or the forces of their pushes were equal).

In at least five horn-locking fights the positions of the two males gradually changed, and one male became less tilted with respect to the substrate while the other became much more tilted, so that his near side legs were out of contact with the substrate and waved ineffectually in the air (Fig. 13). This change in the angles that males made with the substrate was relatively difficult to distinguish and was only noted late in the study; it may have also occurred in other horn-locking fights.

Horn-locking fights often seemed to resolve a conflict. In 43% of 28 battles one of the two males walked away after the fight without any further aggression (and in 21% of the others both males left without further aggression, as the female had moved away while they were fighting). In two taped battles the losing male pulled back and the other remained motionless (it was not possible to distinguish which male pulled away in direct observations).

One further tactic, harassment, was seen on 18 occasions when a small male was displaced from a female by a large male but refused to leave the vicinity, returning immediately each time the large male drove him away. In three harassments the large male succeeded in mounting the female but then dismounted before intromitting to renew his attack when the small male returned. Several times it appeared that the large male repeatedly attempted to align himself for a horn-locking battle, but that the small male, while remaining in front of his opponent, did not align himself properly. Harassment was sometimes successful; in 28% of 18 cases the female turned to oviposit before the large male could copulate with her. In three cases in which the small male eventually left and the large male copulated with the female harassment had lasted a relatively long time (>2 min.).

When a battle of any sort resulted in one male displacing another from a female, the winning male nearly always copulated with the female within 30 seconds (11 of 12 cases in which this time was measured). The one exception illustrated the importance of the quickness

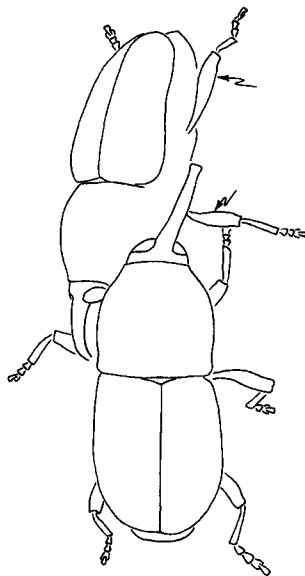


Fig. 13. Dorsal view of a horn-locking fight. The upper male has been tilted and his left rear and middle legs (arrows) wave powerlessly in the air.

of the male's response. The male only attempted to copulate with his newly won mate after she had turned to oviposit, and did not succeed in intromitting until after the egg was laid.

C. Distribution of beetles in the field

Beetles were found both on the cut surfaces of the leaves, where they were more or less continuously active, and wedged immobile in cracks or cavities near these surfaces (see Methods). The average numbers of males and females present on 23 inhabited leaves were 4.96 ± 3.08 and 5.22 ± 3.74 respectively, with maxima of 12 males and 14 females. An average of 30.5% of the males and 29.0% of the females were on the cut surface rather than in cracks. In five less populated fields, the average number of beetles per inhabited leaf ranged from 2.0 to 3.75, and 70.2% of the 148 apparently appropriately aged leaves in these fields had no beetles at all. There was no difference in the prothorax lengths of 141 females collected on surfaces and 345 in cracks (respective averages 0.977 ± 0.082 mm and 0.967 ± 0.084 mm; $p =$

0.24 with t Test). But 141 males on the surface were significantly larger than 321 in cracks (respective average prothorax lengths 1.042 ± 0.103 mm vs. 1.008 ± 0.114 mm, $p = 0.003$; respective average horn lengths for 122 and 272 males were 0.481 ± 0.252 and 0.357 ± 0.256 mm, $p < 0.001$). Analyzing these same data in terms of males on either side of the break point of horn length (0.42 mm), 60.7% of 122 males on the surface had large horns, while only 41.2% of the 272 males in cracks of the same leaves had large horns (Chi Squared = 12.8, $df = 1$, $p < 0.001$).

There were no significant differences in horn or prothoracic lengths of males or in the prothorax lengths of females found on the recently cut leaves that we set out compared with those of beetles on leaves that had been on the ground longer (respective values of p in t Tests were 0.82, and 0.16).

DISCUSSION

Functional morphology

Our observations strongly suggest that the horns of male *Parisoschoenus expositus* function as weapons to lock the male to his opponent and allow him to tilt him during horn-locking battles, and not in other contexts. There was no sign from male behavior that the horns were used as visual or tactile courtship devices. The possibility that females do at least see the horns during courtship and copulation (e.g., Figs. 8, 9) cannot be ruled out, but males never positioned themselves appropriately (broadside to the female) to display their horns visually, as occurs in many horned ungulates (e.g., Geist 1966, 1978; Lincoln 1994). Other possible functions of horns, such as defense against predators or manipulation of food or other substrates, seem unlikely because of both horn design and the absence of horns in females. The function of the otherwise enigmatic pit and internal sheath between the horns is intelligible as an adaptation to use horns as weapons in battles between males, and the dimorphic relationship of horn size with body size occurs in other structures that are used as weapons (Eberhard and Gutierrez 1991; Emlen 1994).

The most extraordinary aspect of the morphology of *P. expositus* is the pair of prothoracic sheaths whose only likely function is to receive and accommodate the horns of other males. Even the beveled edge of

the pit between the horns (Fig. 2) seems designed to facilitate the insertion of an opponent's horn. At first glance it seems paradoxical that a male would have such a structure designed to facilitate the action of an opponent's weapon. But due to the rigidity of both the horns and the sheaths, it is necessary for a male to have a sheath if he is to be able to bring one of his own horns to bear on a similarly horned opponent. The horn plus sheath design thus facilitates apparent tests of strength. Similar locking and subsequent tests of strength occur in the scarabine *Typhoeus typhoeus* (Palmer 1978) and in some ungulates (e.g., Wachtel et al. 1978). The weevils differ from ungulates, however, in that fights do not escalate to damaging battles, and in that the locking structures presumably evolved via selection favoring aggressive rather than defensive abilities (e.g., Geist 1978).

Several details of horn and sheath morphology fit this interpretation. Horns lack the numerous flattened setae that cover most of the rest of the body, and that might impede or be broken off during insertion in the sheath of another male. Similarly, the lack of setae in the region of the pit and on its inner surface would avoid the possibility of their being broken off during horn-locking fights. The smooth, pebbly inner surface of the sheath could facilitate insertion of the opponent's horn. The short setae scattered in small pits over the surface of the horn probably function as sense organs that allow the male to sense whether his horn is inside his opponent's sheath. The greater density of setae near the base of the horn suggests a function in sensing how deeply the male's horn has been inserted, information which may be important at the start of horn-locking battles.

Horn insertion could be advantageous if it somehow increased the male's mechanical advantage in the apparent tests of strength that occur during horn locking battles. One force that seemed to be exerted by fighting males during these battles was a rotatory twist on the opponent. When a male was twisted in this way, he undoubtedly lost most of his ability to push his opponent.

The lateral curve of the horns of large males may function to facilitate twisting the opponent. The lateral curve of a horn would tend to accentuate the tilt of the opponent laterally, lifting his near-side legs from the substrate. Perhaps the additional dorsal curve of the horns of larger males has a similar effect, lifting the opponent's body and thus reducing his ability to push.

Our observations suggest possible functions for several other sexually dimorphic male traits in *P. expositus*. The brush of long setae on the tip of the front tibiae and the tarsi of males probably functions in courtship by modifying the stimuli resulting when the male pats the female during and immediately following copulation. The brush of setae may also modify the stimuli that result when a male is slapped by his opponent in a pushing battle.

The stridulatory structures are moved when males battle with each other, but seldom if ever during interactions with females, indicating that they produce threat rather than courtship signals. Rapid head vibration is apparently a visual threat display when males are not in contact, and a visual or tactile display when they are in head-locking battles.

It is interesting to note that two types of aggressive behavior in *P. expositus* also occur in much more elaborate forms in other weevil species. The front leg slapping resembles the highly stylized "clubbing" blows with the front legs in *Macromerus bicinctus* (Weislo and Eberhard 1989). Prying with the rostrum is similar to the powerful flipping movements of *Rhinostomus barbirostris* that can knock opponents from a log (Eberhard 1983).

Selection on male fighting ability

Several details of the behavior of male *Parisoschoenus expositus* indicate that the last male to mate with a female before she oviposits is likely to fertilize that egg. Males energetically battled over females drilling holes for eggs, but showed little or no interest in females in other contexts, and in fact often abandoned a previously strongly defended female within 10 seconds after she began to oviposit. There is approximately 70-80% last male sperm precedence in the weevil *Anthonomus grandis* (Lindquist and House 1967; Bartlett et al. 1968; Klassen and Earle 1970; Villavaso 1975). These studies involved multiple eggs laid after the final copulation, instead of only one, as in this study, so they are not perfectly comparable. Males of the weevils *Rhinostomus barbirostris* and *Macromerus bicinctus* also compete most intensely for females about to oviposit (Eberhard 1983; Weislo and Eberhard 1989). Given the fact that *A. grandis* sperm in the female's bursa can survive and fertilize eggs, it seems possible that males of *P. expositus* compete for fertilizations by flooding the bursa with sperm

and/or by removing sperm from previous males. Morphological studies of copulation will be needed to resolve this point.

Males were not marked individually in this study, but it seems probable that a large male may sometimes mate up to 5-10 times/hr. Large males may thus have to carefully apportion their sperm. The advantage to large males of transferring sperm only to drilling females, combined with the males' apparent inability to determine reliably and rapidly which females were about to oviposit, could account for the occasional failure of a male to mate soon enough after taking over a female before she oviposited.

If one assumes that the last male to copulate is likely to fertilize each egg, then the numbers of ovipositions immediately following copulations with large and small-horned males, combined with information on the relative abundance of large and small males (216:162 in 388 males), can give a relative estimate of the strength of natural selection on body size and horn length. Large-horned males were the last to copulate 48 times and small males 9, so large males seem to be favored by a factor of about 5:1. It is usual in species with alternative male tactics for large males with more forceful tactics in competition for females to be favored over others (Andersson 1994).

These data are of only limited value, however, regarding the intensity of natural selection on male body and horn size in *P. expositus*. Our behavioral observations were concentrated on palm leaves which had unusually large populations of beetles active on the cut surface, and small males would probably be at less of a disadvantage at lower densities because they would be less likely to be discovered and displaced by a large male once they had found a drilling female. The densities of beetles in the palm plantations may also be unnaturally high or low. Post-copulatory biases imposed by cryptic female choice (Eberhard 1996) or sperm competition (Parker 1970) could make some copulations more likely to result in fertilizations of eggs than others. Finally, the smooth cut surfaces of leaves trimmed from trees undoubtedly increased the ease with which beetles could walk, in contrast with a more natural possible microhabitat such as the broken rachis of leaves snapped by the wind or fallen deciduous bracts of inflorescences. Increased mobility might increase selection against small males by making them more likely to be discovered with a female by a large male before oviposition occurred. The relatively large surface of

potential oviposition sites on cut leaves may, on the other hand, make it more difficult for large males to patrol and thus decrease the strength of selection against small males.

Despite these limitations with respect to quantitative estimates of male reproductive success, our observations nevertheless document qualitatively several reproductive disadvantages of small males. Small males were consistently defeated in battles over females with which the small males had already mated, although in 28% of 18 cases the small male was able to delay the other beetle long enough to allow the female to oviposit before the larger male could copulate. Similar delaying actions by small males were also sometimes successful in *Rhinostomus barbirostris* (Eberhard 1983). Smaller males also suffered interrupted copulations when they interposed their bodies between the female and other approaching beetles, while large males did not interrupt copulation when a small male passed nearby. Probably the greatest disadvantage of small males stemmed from the less dramatic lack of interaction that occurred when a small male came upon a large male defending a drilling female. The small individual almost always simply walked on past, presumably because of his inability to drive the large beetle away or distract him long enough to copulate with the female.

The observations of males briefly following and mounting but then abandoning females that were apparently searching for oviposition sites or that were ovipositing suggested that males have limited abilities to distinguish females that were about to oviposit from others. Males of *Macromerus bicinctus* also appeared to have difficulty distinguishing drilling from non-drilling females (Wcislo and Eberhard 1989).

In some cases it appeared that participating in a long horn-locking fight was disadvantageous even for the winning male. In at least four cases long horn-locking fights were only finally resolved after the female had oviposited her egg (in two of these the female had already started to oviposit when the fight began), and in four others a third, small male mounted the female and attempted to mate while the two large males were battling. The populations of males on a given leaf were relatively small, however, so a given male was likely to have numerous future interactions with the male with which he was battling at the moment. Thus it may pay a male to continue to battle even after the egg laid by a given female has been lost, if by so doing he reduces the chances that his opponent will interfere with his future attempts to

copulate. Similar apparently excessive aggression also occurs in the weevils *R. barbirostris* (Eberhard 1983).

Fights in *Parisoschoenus expositus* were clearly symbolic. No physical harm was inflicted, as occurs, in contrast, in the horned dynastines *Dynastes hercules* (Beebe 1947) and *Allomyrina dichotoma* (Siva-Jothy 1987), and in the armed bug *Acanthocephala declivis* (Eberhard 1998). In addition, even in highly mismatched pairs the larger male was unable to physically remove the other beetle definitively from the vicinity of the female [in contrast with several horned dynastines - Beebe (1944, 1947), Eberhard (1977, 1979), Siva-Jothy (1989); and a tenebrionid - Pace (1967), Brown (1980), Brown and Siegfried (1983)]. A losing *P. expositus* male could (and often did) simply walk back to the female and renew the fight there. The most clearly symbolic fights were the horn-locking battles. These never ended with one beetle pushing the other any great distance. Instead, the two contenders stopped pushing and separated; then usually either one or both left without further ado.

In contrast with another horned weevil, *Centrinaspis* sp. (Eberhard and Gutierrez 1991), there is a clear morphological dimorphism in horn size among males of *P. expositus*. Compared with some horned scarab beetles, however, the two forms are less sharply distinguished and there are more intermediate males (see, e.g., Eberhard 1982; Eberhard and Gutierrez 1991; Emlen 1994, 1997). It is possible that the propensity to defend females by utilizing harassing behavior also differs between large and small males of *P. expositus*. Nearly all extended harassing defenses were performed by relatively small males. Nevertheless, these observations could be the result of a uniform trend in all males to harass only when the other male is substantially larger. Small males apparently do not differ from large ones in engaging in horn-locking battles with opponents of similar size.

The flat frequency distribution of horn sizes in *P. expositus* is similar to that of the horned tenebrionid *Bolitotherus cornutus* (Brown and Siegfried 1983), and males of the scarabeine *Coprophanaeus ensifer* (Otronen 1988), but different from the strongly skewed distribution in *Centrinaspis* sp. and the bimodal curves of several other horned species (Eberhard and Gutierrez 1991). The platykurtotic distributions of horn sizes in *P. expositus*, combined with the clearly normal distribution of body size, imply that there has been selection against males with intermediate horn lengths.

As would be predicted if behavioral dimorphisms have preceded morphological dimorphisms in the evolution of horns (Eberhard 1980), there was also at least one behavioral difference between large and small males. Smaller males were more likely to occur in cracks near cut leaf surfaces than were larger males. The significance of this difference is not clear, however. It appeared that no mating or oviposition occur in cracks. We observed a gecko lizard preying on beetles on the open surface of a cut leaf, and presume that beetles on the surface are at higher risk of predation. One possibility, which can only be checked with additional field work, is that smaller males come out of hiding at times when larger males are less likely to be on the surface.

ACKNOWLEDGEMENTS

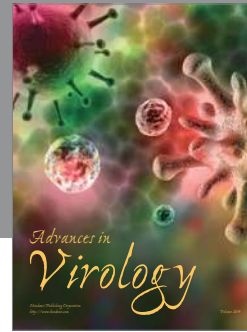
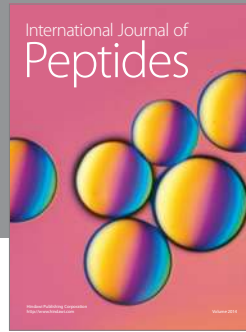
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