Stridulation in the coconut rhinoceros beetle *Oryctes rhinoceros* (Coleoptera: Scarabaeidae)

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Abstract. The coconut rhinoceros beetle *Oryctes rhinoceros* produces different kinds of stridulatory sound under different conditions. Intense stridulations are made quite frequently by the male during courtship and mating attempts. Males also produce characteristic stridulations during aggressive encounters with other beetles, and distress stridulations, when disturbed manually. Females also stridulate, though less frequently. Sexually immature females produce feeble repellence stridulations while courted by males. Gravid females, when confined with males, are found to mimic the courtship and mating behaviour of the males, meanwhile producing intense stridulations resembling male courtship and mating stridulation. This behaviour, presumably has an ovipository motive and, to our knowledge, is the first instance of 'pseudomale' activity to be reported in insects.

Stridulatory mechanism comprises rubbing of a specialised region along the margin of the apex of the elytron—the pars stridens, against a series of striations—the plectrum, occupying the dorsum of the 7th abdominal tergite. Stridulation is possible with a single pars stridens, either of the left or right elytron, both being identical. No sexually dimorphic difference is apparent in the pars stridens. Plectral structure exhibits sexual dimorphism, being much prominent in the male.

Wing-locking is necessary to keep the elytra in the stridulatory position. Locking is effected by a longitudinal flange along the median side of one elytron (either the left or right, irrespective of the sex) fitting into a corresponding depression along the other. This differs from the reported cases in other coleopterans in which the flange of the left elytron extends under the right when locked.

Keywords. *Oryctes rhinoceros*; stridulation; pars stridens; plectrum; courtship.

1. Introduction

During our laboratory studies on the reproductive behaviour of the coconut rhinoceros beetle *Oryctes rhinoceros* it was observed that the sexually activated male beetles/attempting to mate with conspecific females produced loud stridulatory sound quite audible at a distance of about 150 cm. The beetle was found to protrude and retract his apical abdominal segments repeatedly in a rhythmic manner; the tergite of the segment just anterior to the pygidium was rubbed against the inner surface of the elytral tip backward and forward. Instances of elytro-abdominal type of stridulation have also been reported in the white pine weevil *Pissodes strobi* (Harman and Harman 1972), the curculio *Conotrachelus* (Gibson 1967), bark beetles of the genus *Dendroctonus* (Michael and Rudinsky 1972) and in certain scarabaeids (Richards and Davies 1977). In the scarabaeid *Heliocopris bucephalus* sound is produced by another mechanism in which hind coxa is rubbed against the floor of the coxal cavity (Narendran and Joseph 1978). The present paper describes the structures involved in the production of stridulatory sound in the scarabaeid *O. rhinoceros* and also distinguishes different kinds of stridulations as produced by these beetles under different circumstances.

2. Materials and methods

The beetles used for experiments were raised from field-collected third instar larvae sexed as per the method of Mini and Prabhu (1988) and reared individually on sterilized cowdung according to Mini and Prabhu (1985). Adults could be sexed easily by the presence of bare pygidium in the male as opposed to the bushy one in the female (O'Conner 1953; Nirula 1955). Also the pygidium is round in the male and conical in the female (figure 1A, B). From 30 days onwards of their emergence, the adults were fed ripe banana once a week. For this, they were kept singly in containers along with ripe banana slices for one-day and then returned to the medium.

To observe courtship and mating stridulations, each non-mated 40–50-day old male beetle was confined along with a 30–50-day old virgin female inside an open glass container (9 cm height × 7 cm diameter) and watched closely for a maximum of an hour (Expt. I). This was replicated 10 times. Observations were also made with male beetles (40–50-day old) from which: (i) the 7th abdominal tergite was cut off fully; (ii) the elytral apex (that part of the elytra overlying the 7th tergite) was excised; (iii) apex of the right elytron alone was excised; (iv) apex of the left elytron alone was excised; (v) right elytron was excised completely; (vi) left elytron was excised completely; (vii) both hind-wings were excised completely. Five individuals were observed in each category.

To remove the 7th tergite, the beetles were held in hand, their elytral locking disengaged with the help of forceps inserted in between and keeping the elytra and hind wings upwards, the whole tergite was excised along its margin. The hind-wings and whole elytron were also removed in a similar manner. After the operations the remaining wings were brought back to their original position and the wing-locking was reestablished manually (where both elytra remained). The beetles were used for observations 15 min after operation.

To find out the relation between abdominal movements and sound production, dead beetles, 5 males and 5 females (within 24 h after death) were manipulated in such a way that similar movements were reproduced manually. For this purpose the beetles were held between the thumb and index finger and keeping the animal close to the ear the abdomen was pressed slowly and repeatedly to make its dorsum rub against the elytra (Expt. II). This was also repeated with dead beetles after removing their: (i) 7th abdominal tergite; (ii) elytral apex; (iii) right elytron; (iv) left elytron; (v) hind wings. Five males and five females were used in each category.

Female beetles (30–40-day old) were allowed to mate once with non-mated 40–50-day old males by confining them in pairs to the container for a maximum of 1 h daily or until mating took place, whichever was earlier. These mated females, upon reaching an age of 60–80 days were confined singly with 30–50-day old male and observed for 1 h to witness 'ovipository' stridulation (Expt. III). The females were then dissected out and the number of mature eggs counted.

Female beetles attained sexual maturity 23 ± 2 days after emergence (unpublished observation). Immature female beetles, 10–20 days after emergence, were confined each with a 40–50-day old non-mated male and watched for 1 h to observe repellence stridulation (Expt. IV).

To evoke male aggressive stridulation, 40–50-day old non-mated male beetles were confined in pair inside the container and observed continuously for 2 h (Expt. V).

Distress stridulation (Expt. VI) was induced in 40–50-day old non-mated male beetles (i) by holding lightly and touching roughly and repeatedly on their mouth parts with a camel hair brush and (ii) by pressing them hard between thumb and index finger for about 60 s and then releasing them upon table for watching. Experiments III-VI were each replicated 10 times.

Structural details on the dorsum of the 7th abdominal tergite and the inner surface of the elytral apex were studied by observing these parts excised from live beetles of both sexes, 10 males and 10 females, under a binocular dissection microscope. A thin coat of Quickfix (an adhesive cement manufactured by Wembley Laboratories, Delhi) was applied to the surfaces of study after gently scraping off the hairs with a needle, and when dried, film was peeled off to study the impressions cast on it, under the microscope.

The machanism of wing-locking was studied by cutting across the elytra at its stridulatory zone in the locked condition and viewing the cut face under dissection microscope. Ten beetles each from both sexes were used for this purpose.

3. Results and discussion

Results of Expts. I–VI are given in table 1. Male beetles produced loud stridulatory sound during courtship and mating. While making this sound, he was found to exhibit rhythmic abdominal movements in which the penultimate tergite was scraped repeatedly against the elytral apex. Similar sound could be produced in dead beetles by manually reproducing identical movements. However, no sound could be produced in dead beetles and live beetles from which either the 7th tergite or elytral apex was extirpated. Thus it was evident that the sound producing devices were distributed partly on the dorsum of the 7th tergite and partly on the elytral apex and that sound was produced by rubbing one against the other.

3.1 *Structure of the plectrum*

The stridulatory structures associated with the abdominal tergite in different coleopterans have been referred to as plectrum (figure 1A, B) (Dumortier 1963; Gibson 1967; Harman and Harman 1972; Michael and Rudinsky 1972).

In the male *O. rhinoceros* dorsum of the 7th abdominal tergite revealed a striated appearance, being formed of numerous parallel rows of transverse ridges or striations. This area of striations commenced from a little behind the anterior margin and extended up to the posterior margin of the tergite. Laterally it extended about half the distance from the median line on either side and merged with a rather scaly area covered with hairs.

The ridges were highly prominent in the anterior region of the tergite where they were organised into two distinct zones — the zones of major striations (zmas), one on either side of the middle line. Lying medially, and laterally and posteriorly to these zones of major striations, was another zone — the zone of minor striations (zmis). The zones of major striations were formed of thicker, higher and well-separated ridges arranged in 5–12 rows with larger spacing in between. The size of these ridges decreased gradually so as to merge with the zone of minor striations. The zone of minor striations was formed of more closely packed rows of thinner, less higher and discontinuous ridges. There were very few hairs in the plectral region, especially along the mid-dorsal line.

Table 1. Stridulation in *O. rhinoceros* under different conditions.

Expt. No.	Beetle used/ treatment	Kind of stridulation observed	No. of beetles tested		No. of beetles stridulated	
			Male	Female	Male	Female
I	Normal mature male	courtship and mating stridulation	10		10	
	7th abdominal tergite removed from the male	—»—	5		—	
	Elytral apex removed from the male	—»—	5		—	
	Right elytron-apex alone removed from the male	—.»—	5		5	
	Left elytron-apex alone removed from the male	—»—	5		5	
	Right elytron removed from the male	—»—	5		—	
	Left elytron removed from the male	—»—	5		—	
	Hind-wings removed from the male	—»—	5		5	
II	Dead beetles	Stridulation by manipulation	5	5	5	5
	7th abdominal tergite removed from dead beetle	—»—	5	5	—	—
	Elytral apex removed from dead beetle	—»—	5	5	—	—
	Right elytron removed from dead beetle	—»—	5	5	5	5
	Left elytron removed from the dead beetle	—»—	5	5	5	5
	Hind-wings removed from dead beetle	—»—	5	5	5	5
III	Gravid female	Ovipository stridulation		10		6
IV	Immature female	Repellence stridulation		10		7
V	Mature male	Aggressive stridulation	10 pair		3	
VI	Touching the mouth-parts of mature male with hair-brush	Distress stridulation	10		10	
	Pressing the mature male between the fingers	—»—	10		6	

Plectral ridges exhibited sexual dimorphism. In the female *O. rhinoceros*, the zones of major striations were less prominent being formed of smaller ridges less orderly arranged than in the male (figure 1B). In certain *Conotrachelus* species both sexes have identical plectrum (Gibson 1967) whereas in some *Dendroctonus* beetles, only the males have plectrum (Michael and Rudinsky 1972).
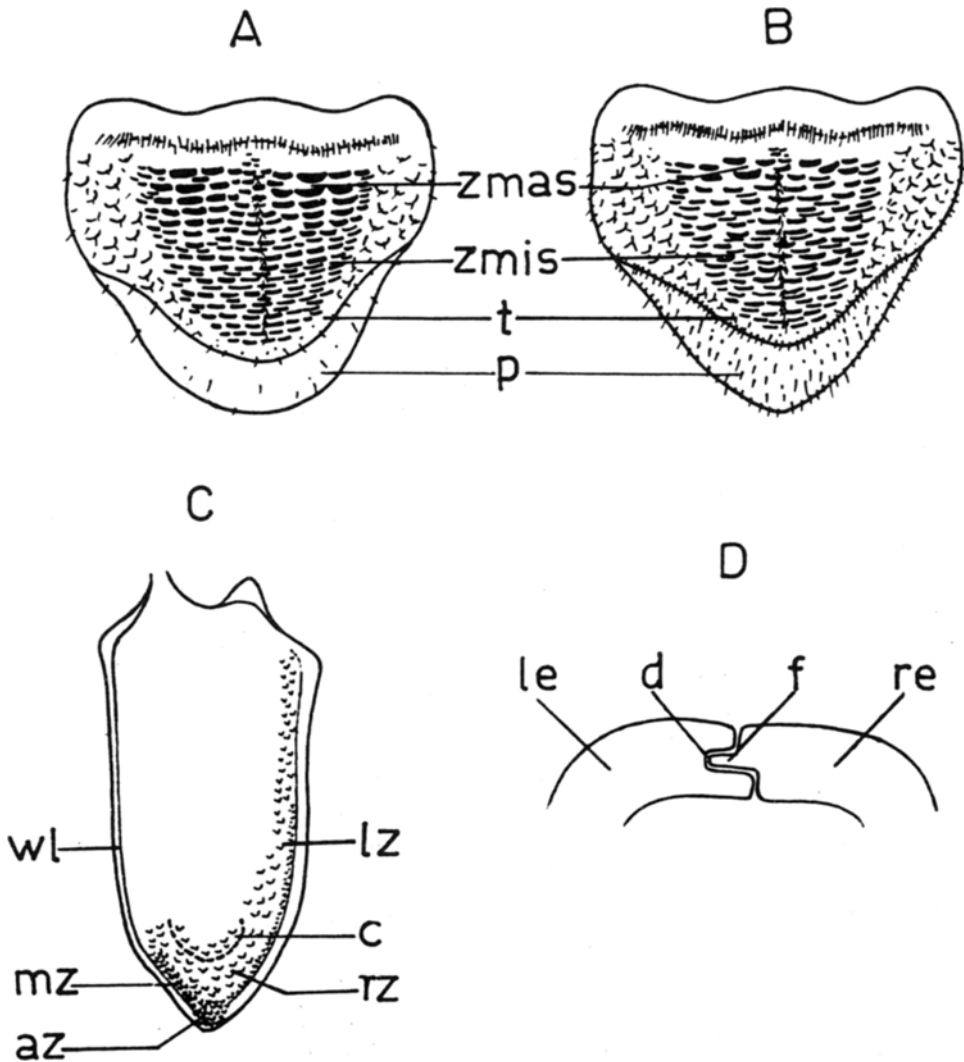
Figure 1. **A.** 7th abdominal tergite of male *O. rhinoceros* beetle showing the plectrum and pygidium. **B.** 7th abdominal tergite of the female showing the plectrum and pygidium. **C.** Left elytron-ventral view (after the removal of hairs). **D.** Cross-section of the elytra showing wing-locking mechanism. (az, Apical zone; c, concavity; d, depression, f, flange; le, left elytron; lz, lateral zone; mz, median zone; p, pygidium; re, right elytron; rz, rough zone; t, tergite, wl, wing-lock region; zmas, zone of major striations; zmis, zone of minor striations).

3.2 Elytral stridulatory structures

The inner surface of the elytral apex in *O. rhinoceros* was covered over with densely arranged posteriorly directed hairs. When these hairs were removed, a rough texture was unraveled; in the apical region of each elytron, there was a rough zone (rz) bearing numerous minute regularly arranged teeth-like projections, lying inner to the smooth rim of the elytron (figure 1C). In the median side of each elytron, this

zone reached only as far as the level of a concavity (c) found towards the elytral tip (mz). In the lateral side, this zone extended anteriorly through the whole length (lz). Towards the rim of the elytron, the teeth were much compactly aggregated and in the apical point of the elytron, this zone of closely packed teeth encroached up to the extreme edge, obliterating the rim (az).

Elytral structures associated with sound production have been described in several coleopterans as pars stridens (Dumortier 1963; Harman and Harman 1972; Michael and Rudinsky 1972) or stridulitrum (Gibson 1967).

When either the left or the right elytron was extirpated, live beetles could produce no stridulatory sound though stridulatory movements occurred normally. This was due to the absence of the wing-locking mechanism which normally kept the elytra firmly engaged with the plectrum during stridulatory movements. When one elytron was removed, the remaining elytron failed to remain in its normal position; it showed a tendency to rise up thus making it impossible to rub against the plectrum. If only the apex of the elytron was excised keeping wing-locking intact, the beetle could produce stridulatory sound with the help of the intact elytron. Sound could also be produced with a dead beetle having either the left or right elytron as this elytron was being brought into contact with the plectrum manually during manipulation. However, in certain male *Dendroctonus* beetles (Michael and Rudinsky 1972) and certain *Conotrachelus* weevils (Gibson 1967), the left elytron is essential for stridulation as the pars stridens is mostly confined to it. The weevil *Pissodes strobi* can however stridulate with a single elytron, either the left or right, since both are provided with closely similar pars stridens (Harman and Harman 1972), as in *O. rhinoceros*.

No sexually dimorphic difference could be observed in the elytral stridulatory areas.

3.3 *Wing-locking*

Wing-locking was effected by a longitudinal flange along the median side of one elytron (either the left or the right, which varied, irrespective of the sex) fitting into a corresponding depression along the margin of the other (figure 1 D). This condition differed from the reported cases in other coleopterans (Harman and Harman 1972; Gibson 1967) in which the flange of the left elytron extended under the right when locked.

The stridulatory areas did not extend into the wing-lock region. So there was no overlapping of stridulatory areas of the two elytra when they were interlocked; they occupied identical positions in relation to the plectrum and contributed equally towards stridulation.

3.4 *Role of hind-wings in stridulation*

Hind-wings were not essential for stridulation. Even after both hind-wings were removed, live beetles, and dead beetles upon manipulation, could produce stridulatory sound though the sound was distinctly different from that produced when hind-wings were present.

The left hind-wing was suspected to be functioning as a bridge or resonator in *Conotrachelus* (Gibson 1967). In *O. rhinoceros* the hind-wings were kept folded

beneath the elytra leaving a 'Λ' shaped gap between the folded apices through which the plectrum could communicate with the elytra; this space might have served as a resonating column.

3.5 Mechanism of sound production

During protraction of the last few abdominal segments (6th-8th), the plectral ridges scraped against the elytral apex producing a pulse of sound. During the subsequent retraction of the abdominal segments the plectrum again engaged the pars stridens, producing another pulse of sound. These two pulses produced during the forward and backward strokes together constituted a chirp. As the strokes were repeated varying number of times, a series of chirps (2–5) were produced at a single stretch constituting a chirp-series. The number of chirp-series produced by a courting male before achieving copulation varied from one to several.

The mechanism of sound production in *O. rhinoceros* is similar to that reported for certain cerambycids (Finn *et al* 1972).

3.6 Different kinds of stridulations

Stridulations that are of sexual significance have also been reported in a number of other coleopterans (Barr 1969; Claridge 1968; Mampe and Neunzig 1966; Michael and Rudinsky 1972; Wilkinson *et al* 1967). Apart from the courtship and mating stridulations, male *O. rhinoceros* were also found to produce stridulatory sound during aggressive encounters with other males. However, such aggressive stridulations could be observed very rarely, while observing male beetles confined in pairs inside the container. There were 3 instances during which the males met head-to-head and exerted pressure upon each other aggressively, with one or the other making abdominal movements associated with stridulatory sound. Such aggressive stridulations were different from sexual stridulations. Here the backward and forward strokes were separated by a detectable pause; also, the strokes were longer. These observations are in step with the audiospectrographic data from *Conotrachelus carinifer* (Gibson 1967) in which slower and more deliberate stridulations have the backward and forward strokes separated by a pause; in these, more stridulatory ridges per stroke are involved. In *Dendroctonus pseudotsugae* also, stress stridulation is different from sexual stridulation (Rudinsky and Michael 1972).

Live males could be induced to stridulate by touching forcefully on their mouth parts with a camel hair brush. Such distress stridulations were very feeble and short, resulting generally from a forward and a backward stroke coinciding with each stimulus and it could be detected only at close range. However if the beetle was pressed hard and then released, many made a series of chirps, closely resembling courtship stridulation. There was a time lapse of the order of a few seconds between the release of pressure and stridulation. Distress stridulations have also been reported in *Conotrachelus* (Gibson 1967) and *D. pseudotsugae* (Rudinsky and Michael 1972).

Thus, as reported for some other coleopterans (Finn *et al* 1972; Michael and Rudinsky 1972) *O. rhinoceros* was also capable of producing different kinds of stridulatory sound varying in intensity and duration, ranging from mild chirps

detectable only at a very close range to loud chirps detectable at a distance of about 150 cm.

3.7   Stridulation in female beetles

Female *O. rhinoceros* also stridulated, though less frequently. Young virgins (30–40-day old) did not stridulate while being courted by the male. However, mated females (60–80-day old) produced stridulatory sound comparable to male courtship and mating stridulation while they interacted with the males. These females chased the males, mounted them and exhibited rhythmic abdominal movements producing intense stridulatory sound, all in an exactly male-like manner. This behaviour, which could be regarded as 'pseudomale' behaviour, apparently enabled the female to circumvent the courting attempts of the male. However, there were several instances in which the females initiated this behaviour though there were no courtship threat from the males. One such female who was stridulating after mounting a male protruded the vagina and ejected out an egg along with the rhythmic abdominal movements. These observations together with the fact that this behaviour was exhibited only by gravid females suggested an 'ovipository' motive operating behind this behaviour. All these females when dissected revealed a number of mature eggs (9–18, with an average of 13·8 eggs). Stridulation by such gravid females may hence be regarded as 'ovipository', presumably having some link with oviposition.

Sexually unreceptive immature females (10–20-day old) when courted by the males, were sometimes found to make abdominal movements similar to that during stridulation. Feeble sounds could be heard at very close range; successive abdominal thrusts were widely separated. That is, instead of a series of backward and forward strokes occurring in rapid succession characteristic of 'ovipository' stridulation, there were isolated strokes during this repellence response, and these strokes were repeated at irregular intervals.

Acknowledgement

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