The Natural History of Doryphora sp. (Coleoptera, Chrysomelidae) and the Function of its Sternal Horn

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ABSTRACT

The beetle Doryphora sp. near punctatissima uses its sternal horn as a weapon in intra-specific aggressive encounters on the food plant Prestonia isthmica Woodson where eggs are laid and larvae and adults feed. Eggs are laid in groups and hatch in about a week. Larvae complete development in groups, and sometimes consume all leaves on a host plant. Larvae burrow into the soil to pupate; adults emerge in about 24 days. Adults display little apparent courtship behavior; mating can last longer than 1 hour and females apparently mate more than once. Aggressive behavior of adults is most likely related to defense of the food plant.

Doryphora sp. near punctatissima is a large chrysomeline beetle with a short, slightly curved, forward-projecting horn arising on its mesosternum (Fig. 1). There is no marked sexual dimorphism, and the horns of males and females are indistinguishable. Since the unusual position and size of the horn suggested that it might be an exception to the apparent tendency for beetle horns to function as weapons (e.g. Eberhard 1979, 1980), a study of the beetle in its natural environment was undertaken. The results, which include data on the behavior and ecology of the immature stages as well as that of the adults, are presented here.

Study Site and Methods

Field observations were made early in the rainy season (May) of 1978 in a weedy pasture and a cleared field which had recently been overgrown with weeds at the edge of El Porvenir, Meta, Colombia. The area, which is within the flood channel of the Rio Meta, is classified as dry tropical forest in the Holdridgian life zone system (Espinal and Montenegro 1963). Additional observations were made on beetles kept in jars and cans at the “Chenevo” ranch about 25 km to the SE. Observations by M. Barreto in July confirmed that adults were still present at this site later in the season.

Beetle specimens were identified by Richard E. White, and voucher specimens of adults, pupae, and larvae are deposited in the U.S. National Museum. The food plant was identified by Luis Fournier, and vouchers have been placed in the collection of the Universidad de Costa Rica.

Results

Food Plant.—The host plant, Prestonia isthmica Woodson (Apocynaceae) grew as a small vine, with some aboveground vines joined by underground runners. This plant was relatively common in some parts of the fields, but scarce in others. Even where it was most common, individual aboveground plants were often one to several meters from their nearest conspecific neighbors.

Eggs.—The yellowish, oval eggs were covered with a clear gummy substance, and were laid in clutches of variable size (\( x = 32.9, \sigma = 12.2, N = 33 \)) on the undersides of leaves of P. isthmica. Most eggs were laid side to side with their long axes perpendicular to the leaf surface, with a few additional eggs laid across the top of the mass oriented so that their long axes were parallel to the leaf surface. A few eggs were infertile in some masses, but there was no obvious difference between the fertility of the top eggs and that of the others. The duration of the egg stage was not determined precisely, but must be more than 7 days since one mass collected in the field hatched 7–9 days later.

The eggs were readily accepted as food by both adult and larval beetles. Egg masses with some or all of the eggs eaten were common in the field (24% of 78 unhatched masses in the field had some damage). Larvae may routinely eat some of the eggs in the mass from which they emerge. Hatching was often not synchronous over the entire mass. Larvae kept in captivity with their egg masses eliminated the empty shells except for the basal ends (similar vestiges of masses were seen in nature), and were also observed to chew unhatched eggs. When masses of 36, 28, 23, and 56 eggs were hatched in captivity, the final numbers of first stage larvae resulting from these masses were 17, 15, 22, and 43 respectively (average loss of 9/mass or 25%). On five different occasions in the field I found larvae apparently feeding on unhatched eggs.

Larvae.—Hatching was observed once under a dissecting microscope. Larvae, which in most cases faced toward the free end of the egg (away from the leaf) did not appear to move as the egg shell split along either side of the thoracic region. Examination of newly emerged larvae revealed a series of three small black spines (which, along with the tips of the mandibles, were the darkened parts of emerging larvae) on the meso- and metapleura and the side of abdominal segment I. Presumably these spines assist in splitting the egg chorion; they were not present on later instars.

Comparisons of a series of larvae indicated that there were four clear size classes which probably correspond to four larval instars. Diameters of head capsules (average \pm standard deviation in mm.) were 1.15\pm0.03 (N=29), 1.81\pm0.08 (N=81), 2.84\pm0.14 (N=58), and

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4.32±0.15 (N=5). The average increase from one instar to the next was 56%, somewhat high compared to other beetles but not surprising considering the large size of this species (Enders 1976).

Larvae were found in the field only on P. isthmica vines, although cursory searches were made on nearby species of plants. First stage larvae fed on only one half of the thickness of the leaves of P. isthmica, while larger larvae fed at the edge and ate the entire leaf. Typically, larvae started near the tip of a leaf and worked toward the base, eating the central vein along with the rest. In one plant which had been completely stripped of leaves, larvae also fed on the epidermis covering the central stem of the vine.

Larvae gradually changed color as they matured. New first instars were black and grey, while the grey color was usually replaced by an increasingly intense red in larger individuals. Larvae raised on beetle eggs in captivity turned yellow rather than red. There was some variation in color and some individuals of the same size within a single group in the field had distinctly different coloration.

When disturbed, larvae regurgitated a dark brown liquid. Despite the animals' aposematic coloration, I did not sense any unpleasant sensation other than a slight roughness in the throat when I tasted blood, viscera, and the rest of the body.

Larvae were typically found in groups rather than dispersed, with group sizes ranging from 2 to 40. On five plants there were groups of larvae of distinctly different sizes, presumably as a result of the mixing of different broods, but all of the other 46 groups observed were of individuals of similar sizes, suggesting that a group is usually derived from a single clutch (the generally wide spacing of host plants would seem to preclude substantial migrations of larvae from one plant to another).

Mortality in the larval stage (assuming negligible migration of larvae between plants) was suggested by the fact that the average number of individuals per group of first and second instars was 10.2, while that of groups of larger individuals was 7.7. These averages were not statistically different due to the very pronounced variations within each age group, but are both statistically smaller than the average number of eggs per clutch. These variations within age groups (coefficients of variation were .99 and .75 as compared to .37 for number of eggs/mass) suggest widely variable success for different clutches.

In contrast to eggs, larvae were not accepted as food by either other larvae or by adults, at least in trials in captivity in which individuals known to have been without food were left for several days with small larvae.

Pupae.—Large larvae in captivity burrowed into the sandy soil and pupated. The duration of the pupal stage was not determined precisely, but soft new adults were present in a container 24 days after the first of 7 larvae burrowed.

Adults.—I was particularly interested in the functions of the beetles' horns, and observed several aspects of adult behavior in hopes of seeing the horns put to use.

Feeding.—Adults of both sexes fed on the leaves of P. isthmica, chewing their edges with their strong mandibles. The horns did not make contact with the leaf.

Defense.—When held in the hand, the beetles often regurgitated a brownish fluid similar to that produced by larvae. They also bit with their mandibles. They did not make clear attempts to press objects they had seized in their mandibles against the tip of the horn, and the horn thus seemed not to function defensively.

Courtship and mating.—Courtship and mating were observed in nature by placing previously captured males on plants near other adult beetles. The protruding male (or sometimes the resident if it was male) usually mounted the other beetle. There was little or no courtship prior to mounting. Males appeared to detect other individuals from 5–10 cm away, and simply approached and climbed onto them. Once mounted, the male extended his genitalia and probed near the posterior end of the other individual. Occasionally a male shook a few times (almost a shudder) before attempting intromission. Mounted females eventually opened the tips of their abdomens to permit intromission. Copulation occurred with the male remaining on the female's dorsal surface, and lasted in several cases for more than 85 minutes. Females may copulate more than one time, as one individual which was placed with a male on two successive days copulated both times. At no time during any observed copulation were the horns of either individual in contact with the body of the other.

When a male mounted another male and began probing with his genitalia, the mountee often "stilted," extending his legs to raise his body away from the substrate. The mounter usually continued to probe until the mountee apparently opened the tip of his abdomen; after a brief insertion, the beetle on top withdrew his genitalia and dismounted.
Aggressive behavior.—Aggressive behavior, which followed or formed a part of the homosexual behavior just described, was observed in several cases when a male was placed on a plant near another male. In each case one male mounted the other as described above and then dismounted and attempted to push the other beetle away. The male being pushed crouched close to the substrate, while the attacking beetle used his horn as a lever to raise his opponent and thus make him easier to push. The behavior in one particularly intense interaction was as follows: The resident male mounted, then dismounted and immediately began to push against the other with jerky movements. He repeatedly slid the tip of his horn downward over his opponent's dorsal surface until it hooked under his lateral margin, then pushed forward. The intruder was unable to hold his ground, and turned and walked a short distance away; when the resident followed, the intruder turned and mounted him. The resident was quiet while the other was on his back, but renewed his attack even more strongly when he dismounted. The intruder attempted to defend himself by tilting his nearly hemispherical body toward his opponent and thus reduce the purchase the other could get on his smooth body. The resident however repeatedly slid his horn over the other's back until it caught under either the lateral or posterior edge of his elytra or prothorax, then thrust forward strongly by pushing with his hind legs while his front legs were on the dorsal surface of the opponent (Fig. 2). When the horn slipped out of a spot where it had been wedged on the intruder's body, the attacking male jerked forward, thus indicating that he was applying substantial force to his opponent. The pushing attacks were successful and caused the intruder to retreat, with the resident following and giving further sharp thrusts with his horn hooked under the rear of the other's body.

Density of Beetles Relative to that of Food Plants.—*Prestonia isthmica* generally had few leaves per above ground plant ($\bar{x} = 10.7$ pairs, range 2–41, $N = 124$), and even the smallest life stages of the beetles were readily visible, so it was possible to make reliable censuses of all stages in the field; this was done on the 6th, 11th, and 16th of May. The beetles were relatively scarce compared to their food plants. The percentages of plants with eggs, larvae, and adults present were only 37, 34, and 18 respectively.

There was a significantly greater tendency for eggs and larvae to be present on larger plants (adults showed a similar tendency but the sample was small and the differences were not significant) (Fig. 3). These differences could be due to larger plants having been available longer for colonization, but for eggs the differences are probably due to discrimination of ovipositing females since eggs are present for about a week, and thirteen tagged plants grew on the average only 0.1 new leaf pairs per day when followed over a three day period. Whether the differences were due to larger plants simply being easier for beetles to find or whether beetles actively rejected smaller plants is not clear; the fact that the numbers of egg masses per leaf pair were relatively constant (.048, .061, .062, and .060 respectively for the categories of plant size in Fig. 3) could be interpreted as being in accord with either hypothesis.

Discussion

The apparently purposeful and successful use of the horn in aggressive encounters, its appropriate design as a lever for overcoming the defensive behavior of opponents, and the fact that the horn was never observed to be used in feeding, defense, courtship, or mating suggests that the horn is used in intraspecific aggressive encounters. This conforms to the described for other horned beetles (Eberhard 1977, Palmer 1978, Eberhard 1979 and references, Eberhard 1980).
The horn in *Doryphora* sp. and its use differ from those of other beetles in that they are not designed to raise the opponent's center of gravity above that of the attacker (Eberhard 1979); in fact the attacking beetle climbs partly onto its opponent's back, and it is usually the attacker's center of gravity which is higher. This tactic, which would be counterproductive in head-to-head pushing matches like those of many beetles, is apparently effective in *Doryphora* sp. because the attacker usually pushes at the side or rear of the opponent and thus usually runs no risk of being pushed strongly himself as he attacks. In the one case in which I saw a beetle push at the anterior end of another, the second beetle responded by pushing forward and dorsally himself, and both beetles fell from the plant to the ground.

The resource disputed in aggressive encounters is not certain. Since larvae occasionally strip food plants and eat the normally unused shoot epidermis, food may be a limiting and thus valuable resource for which it would be adaptive to fight. That beetles may choose larger plants as oviposition sites also argues in favor of limitation by food. This could explain the presence of horns in both males and females. The ready acceptance of eggs as food by both adults and larvae also raises the possibility that beetles compete by eating each other's eggs. Again ability to fight and drive others from a food plant could be adaptive.

Whether food plants were or are limiting under the conditions in which this species evolved is perhaps unknowable, however, as it would presumably depend on beetle and plant population densities, and egg and larval mortalities, all of which could be influenced by human modifications of the beetles' habitat (now widespread in the area studied). Certainly the relative abundance of uninhabited plants makes it seem unlikely that they are now a strongly limiting resource for the beetles, at least in the season in which this study was conducted.

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**REFERENCES CITED**


