Spray Aiming in Bombardier Beetles: Jet Deflection by the Coanda Effect

Abstract. *Bombardier beetles of the carabid subfamily Paussinae have a pair of flanges, diagnostic for the group, that project outward from the sides of the body. Behind each flange is a gland opening, from which the beetles discharge a hot, quinone-containing secretion when disturbed. The flanges are curved and grooved and serve as launching guides for anteriorly aimed ejections of secretion. Jets of fluid, on emergence from the gland openings, follow the curvature of the flanges and are thereby bent sharply in their trajectory and directed forward. The phenomenon is illustrative of the Coanda effect, widely applicable in engineering and responsible for the familiar tendency of liquids to curve around spouts and down the front of containers when being poured.*

When a liquid or gas flows along a curved surface, it tends to cling to the surface and follow the curvature. This effect, named for the aircraft pioneer Henri Coanda, has application in fluidics and jet technology (*1*). In everyday life it accounts for the annoying propensity of liquids to curve around spouts and lips of vessels when being poured and to trickle down the outside of the containers. We here report what we believe to be the first example of a biological mechanism that operates on the Coanda principle. The case involves certain beetles (family Carabidae; subfamily Paussinae) that eject a defensive fluid when disturbed and depend on the Coanda effect for the aiming of their discharges. Diagnostic for the Paussinae are a pair of flanges (Fig. 1, arrow) of previously unknown function that project outward from the posterolateral margins of the wing covers (elytra) (*2*). We have shown these flanges to be curved, fluid-directing devices that serve as launching guides for the anteriorly aimed discharges.

The Paussinae have fundamental similarities with that remarkable group of beetles known as bombardiers and should probably be designated as such (*3, 4*). The species traditionally called bombardiers are members of a different category of Carabidae, the Brachinini. whose defense mechanism is well known. Brachinines discharge hot benzoquinones (100°C), which they generate explosively by oxidation of hydroquinones in a pair of two-chambered glands specially adapted for such synthesis (*5, 6*). Paussines have comparable two-chambered glands and also discharge benzoquinones (*3, 4*). Moreover, thermal measurements that we made of the spray of one species (*Goniotropis nicaraguensis*) have shown the fluid to be hot (*7*), suggesting that these beetles too produce their quinones by explosive synthesis. But paussines and brachinines differ in how they aim their spray. Whereas in brachinines the two glands open close together on the tip of the abdomen and aiming occurs by rotation of the aodominal tip (*8*), in paussines the glands open anterior to the abdominal tip and aiming occurs by involvement of the flanges, which are entirely missing in the brachinines. We studied the paussine defense mechanism in beetles that we obtained live from Panama. Except where otherwise specified, our observations were made with *G. nicaraguensis* (*9*).

Visual indication of the aiming ability of *Goniotropis* was obtained by causing tethered individuals to discharge on a chemical indicator paper (*10*) in response to mild pinching of legs or antennae with forceps. The prompt, accurately directed discharges issued invariably from only the gland of the side of the appendage stimulated (Fig. 2, A and B).

High-speed motion pictures (400 frames per second) taken of beetles in dorsal and profile view gave a first indication of the role of the flanges. As is seen in Fig. 1 [which is based on analysis of filmed discharges ($N = 90$) elicited by stimulation of hindlegs and forelegs of 17 *Goniotropis*], when the beetle ejects toward the rear appendage, it does so by depressing the abdominal tip slightly and spraying obliquely downward. When, on the other hand, it discharges toward a foreleg, it maintains the abdominal tip appressed against the elytra, and the ejection takes place forward, over the flange and onward in parallel to the body. There was no deviation from parallelism in these forward shots ($N = 60$) (*11*). A close-up motion picture of the posterior portion of the abdomen of an individual of a larger species of paussine (*Ozaena magna*) showed clearly that the jet of fluid in an anteriorly directed discharge is literally bent into its final trajectory by adherence to the outer curvature of the flange. Figure 2G, taken from this film, visibly attests to the potency of the Coanda effect. The jet of fluid, initially directed outward from the body, is deflected angularly more than 50° by the flange.

Destruction of flanges resulted in predictable misdirection of discharges. One flange in each of four *Goniotropis* was almost entirely shaved away with a microscalpel (*12*), and the beetles were then tested for aiming ability by tethering them and causing them to discharge on indicator paper in response to stimulation of forelegs. In each case the discharges from the side of the intact flange were directed forward accurately, while those from the operated side were misdirected with a distinct outward bias. Motion pictures made of one such operated beetle permitted measurement of the degree of angular misdirection resulting from flange ablation. The dashed line in Fig. 1 is the actual tracing from a film frame of the spray trajectory of a forward discharge from the flangeless side of that beetle.

Scanning electron microscopy revealed some of the finer details of the

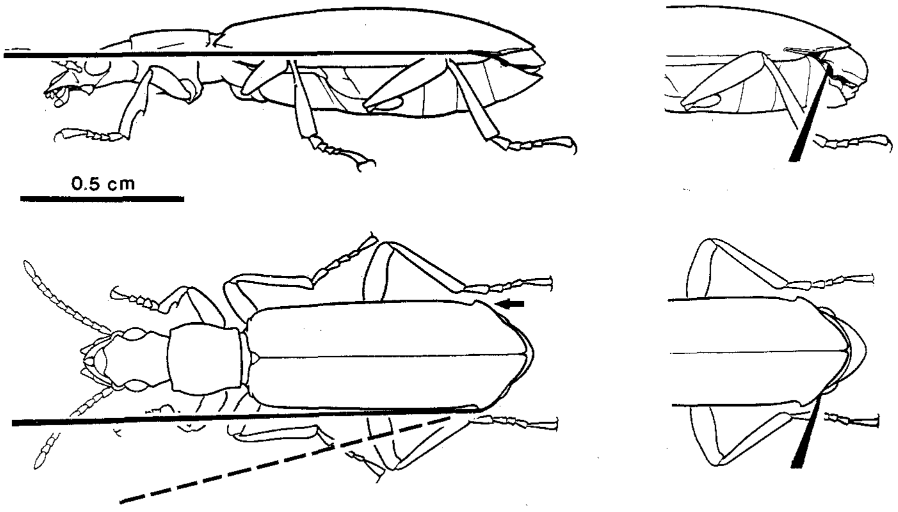

Fig. 1. *Goniotropis nicaraguensis* discharging in response to stimulation of left foreleg (left) and hindleg (right); arrow denotes elytral flange. The dotted line at lower left indicates direction of discharge in a beetle whose left flange has been dissected away.

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flanges and of the gland openings and associated skeletal structures. The curvature of the flange and the groove that follows the curve and provides the pathway for the jet of fluid are clearly depicted in Fig. 2, E and F. In order to obtain a precise view of the relationships of the terminal abdominal structures during forward and backward discharges, two beetles were killed and immobilized for electron microscopic examination at moments when one was discharging toward a foreleg and the other toward a hindleg (*13*). As is apparent from Fig. 2C, during execution of the forward discharge, when the abdominal tip is pressed upward against the elytra, the gland opening assumes a position immediately adjacent to the flange. Due to the tight fit of the base of the flange against its adjoining skeletal structures, there is virtual continuity in the grooved pathway of egress that leads from gland opening to flange. Smooth delivery of fluid to the flange is thus assured. During discharges to the hindleg (Fig. 2D), the abdominal tip is deflected downward, and due to the consequent separation of skeletal parts, the gland opening is disengaged from the flange and raised above what might otherwise be an obstructing "lower lip" (Fig. 2D, arrow). This and possibly other subtle rearrangements (there could be internal orientational shifts of the gland relative to the opening) cause the secretion to be discharged downward, without chance of being diverted to the flange.

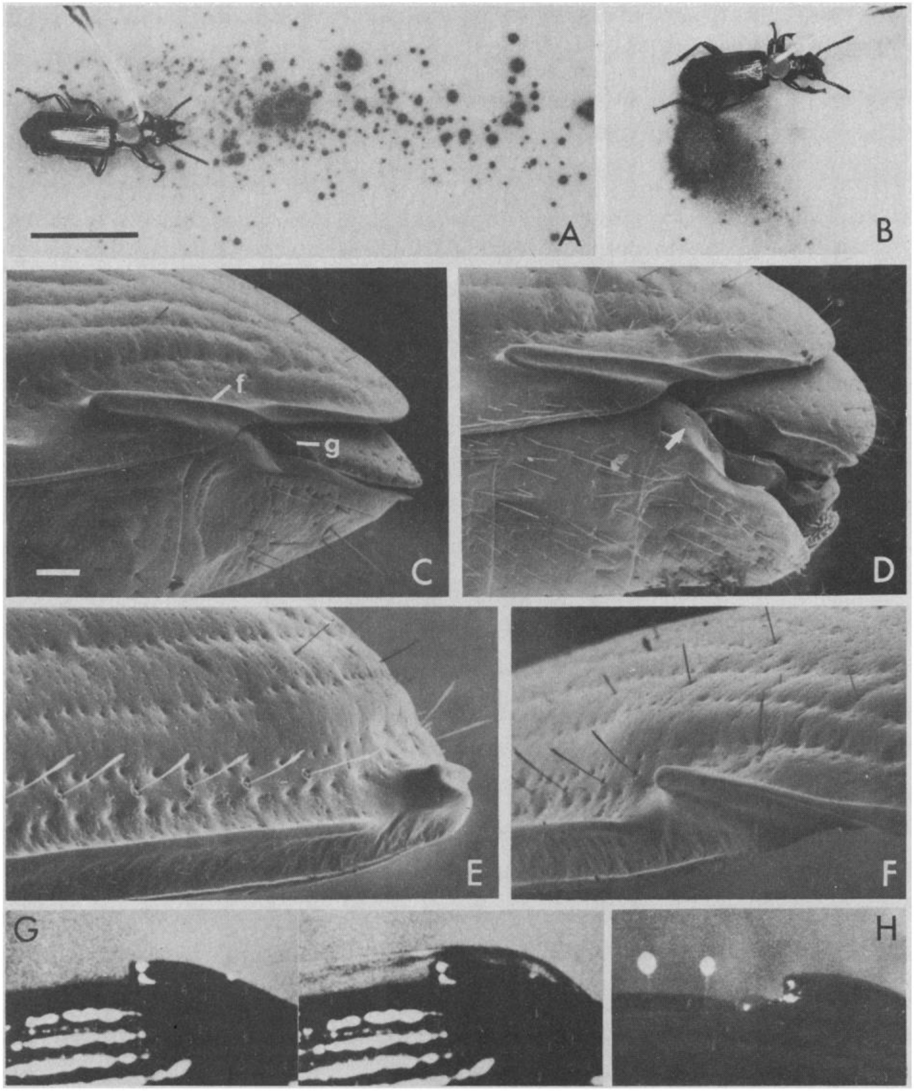

Fig. 2. (A and B) Beetles discharging on chemical indicator paper in response to stimulation of left foreleg (A) and right hindleg (B). (C) Tip of abdomen in lateral view of beetle immobilized while discharging toward a foreleg (*g*, gland opening; *f*, flange). (D) Same, of a beetle immobilized while discharging toward a hindleg [arrow denotes "lip," lowered in (D) from its position in (C)]. (E) Posterior half of elytron in oblique lateral view, showing curvature and groove of flange, and row of hairs aligned along direction of emergence of spray from flange. (F) Same, in different orientation. (G) Consecutive frames of a motion picture showing flange before (left) and during (right) spray ejection; note sharp deflection of jet of spray as it follows curvature of flange. (H) Droplets of secretion taken up by hairs in front of flange (picture taken immediately after a discharge). (A to F and H) *Goniotropis nicaragüensis*; (G) *Ozaena magna*. (C to F) Scanning electron micrographs. Reference bars: (A) 1 cm; (C) 200 μm.

Along the outer margin of each elytron of *Goniotropis*, and precisely aligned with the trajectory of emergence of the spray from the flange, is a row of hairs, terminally spatulate, and in that respect unlike any other hairs on the beetle (Fig. 2, E and F) (*14*). These hairs appear to have the dual function of promoting scatter of secretion when hit by the spray and of retaining droplets of fluid on their flared tips after a discharge. The first function remains speculative (*15*), but the second was verified: in both still and motion pictures droplets were often seen to be left clinging to the hairs after forward discharges (Fig. 2H) (*16*). It was also noticed that the beetles frequently wiped such droplets away following a discharge by use of the mid- and hindlegs, which they drew in precisely directed motions (using tibiae and tarsi) across the elytral margins. The inevitable secretory wetting which the legs must receive as a result of such activity could obviously have defensive value. It was also not uncommon for beetles to be seen to wipe the elytral flanges after discharges, as might well be necessary for maintenance of the operational effectiveness of these structures. In a motion-picture sequence of this behavior, the tarsus of a hindleg of *O. magna* is seen to be drawn precisely over the outer margin of a flange.

Measurements from high-speed motion picures of *Goniotropis* (analyzed on a frame-by-frame basis; 2.5-msec frame interval) permitted calculation of the duration (12 ± 1.2 msec; *N* = 15) and velocity (240 ± 14 cm/sec; *N*=9) of the discharges (*17*). The velocity value was confirmed by independent ballistic measurements (250 ± 28 cm/sec; *N* = 9) (*18*). At such speed of propagation the spray traverses a beetle length of 1.5 cm in 6 msec and a distance of 10 cm (a common range in forward discharges) in about 40 msec.

Tests with ants left no doubt that the defenses of paussines are effective, as those of brachinine bombardiers were already known to be (*8*). Individual *Goniotropis* fastened to tethers were introduced into small laboratory arenas containing groups of ants of an aggressive species (*Formica exsectoides*). The beetles were promptly attacked but, as was clear from direct observations and motion pictures, they consistently discharged when bitten by the ants, causing these to release their hold and flee. Targeted ants were sometimes noticeably contaminated with secretion, attesting to the accuracy of the discharges. Pinching with forceps had shown beetles with replete glands (previously undisturbed for at least 2 weeks) to be capable of discharging upward of 15 times before exhaustion of their reserves. However, in the tests with ants the beetles were only rarely forced to discharge in rapid succession, since each ejection was followed by a period of relative invulnerability during which approaching ants were apparently repelled by residual secretion remaining on the beetle from the previous discharge. Benzoquinone vapors are potently deterrent to ants, and protracted postdischarge invulnerability had also been noted in tests with brachinines (*8*).

Goniotropis and *Ozaena* belong to the Ozaenini, one of two major subdivisions of the Paussinae. The other subdivision, the Paussini, includes species highly specialized for life in ant colonies (*2*). Although they too discharge benzoquinones (*3, 4*), no one knows how their defenses figure in their interactions with enemy or host. But they too have elytral flanges, which we presume to be functionally analogous to those of the Ozaenini.

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7. The technique involved causing the beetles to discharge on precalibrated heat-sensing devices (thermocouples and microthermistors), as previously described for brachinine bombardiers (*5*). The temperature of the *Goniotropis* spray was 65° ± 5°C ($N = 10$) with a maximum of 81°C.
8. T. Eisner, *J. Insect Physiol.* **2**, 215 (1958).
9. Adult paussines are insectivorous; we maintained them for months in the laboratory on pieces of freshly killed mealworms (larvae of *Tenebrio molitor*).
10. The specifications of the paper are given elsewhere (*8*).
11. Omitted from Fig. 1 is an indication of the splatter that often occurred in forward discharges (particularly in the more massive first discharges of beetles with replete glands, as in Fig. 2A). This splatter was a consequence of (i) spontaneous breakup of the jet of fluid as it shot ahead beyond the length of the beetle, and (ii) impact of the jet with legs, antennae, and (when the beetle's body was not held straight) the margins of head and thorax. There was also usually some splatter from the gland opening itself.
12. Flange removal stopped just short of the margin of the elytron.
13. Each beetle was seized by its respective leg and, while discharging (the discharges are faintly audible and can be spotted by the appearance of brownish secretion on targeted appendages), was killed by abrupt immersion in chilled (−195°C) liquid Freon. It was then transferred while still frozen to the precooled stage of a tissue freeze-drier for desiccation and given a conventional metallic coating for electron microscopic examination.
14. *Goniotropis nicaraguensis* is the only species of those listed in our previous chemical papers (*3*) that has the hairs.
15. A scatter of microdroplets from the hairs would not have been resolved at the magnification of our motion pictures; only coarse scatter from other body parts was detectable (*11*).
16. The hairs may also provide sensory feedback from the spray; however, they are rigidly attached at the base and are not movably inserted into sockets as mechanoreceptors usually are.
17. Duration was calculated from counts of consecutive film frames in which individual discharges remained visible, and velocity by measurement of the distance advanced by the leading edge of the jet of spray in consecutive frames.
18. For the ballistic calculation, beetles fastened to rods were adjusted in horizontal stance (direction of emission of spray from flange is then also horizontal) on sheets of indicator paper and caused to discharge forward in response to pinching of forelegs. Spray velocity (v) was calculated from $v = D/\sqrt{2d/g}$, where D is distance from flange to remotest point ahead of beetle where paper was marked by secretion; d is height of flange above paper, and g is acceleration due to gravity.
19. This study was supported in part by NSF grant PCM 77-15914 and NIH grant AI-02908. We thank Drs. R. E. Silberglied and A. Aiello for collecting the beetles (Barro Colorado Island, Canal Zone), T. L. Erwin for identifying them, Susan Poulakis for the drawings, and Professors Sydney Leibovich and Richard Rand of Cornell's College of Engineering for helpful comments. This is paper 68 of the series "Defense Mechanisms of Arthropods."

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Play Behavior: Persistence, Decrease, and Energetic Compensation During Food Shortage in Deer Fawns

Abstract. White-tailed deer fawns continued to play despite an experimentally induced 33 percent milk shortage. They reduced play by 35 percent and general activity by 9 percent but increased grazing by 62 percent, resulting in virtually complete energetic compensation. This demonstrates the importance of play behavior in a mammal's activity budget.

The bioenergetic priority of play behavior in immature mammals has been a matter of dispute ever since Spencer (*1*) postulated "energy surplus" as the proximate source of play. Since long-term effects of play (or its absence) are difficult to measure, the magnitude of the selective advantage (but not its specific nature) of play could be estimated by how much the growing organism is willing to pay for being able to play, especially under energetically adverse conditions. Will play be dropped for short periods and without ill effects? Is it a built-in reserve activity, "behavioral fat" (*2*)?

We report the redistribution of energy allocated to various activities by young mammals when receiving a reduced amount of milk. They continued to play, but at a lower rate, which was proportional to the food reduction. They spent more time resting but increased their grazing drastically. These adjustments resulted in only minor changes of both the energetic input and output.

Play behavior comprises vigorous activities, such as leaping, running, chasing, striking, or wrestling, in the absence of an immediate need for fleeing or fighting. It can be solitary, parallel (that is, socially facilitated without interaction), or social (that is, interactive). Many adaptive functions have been postulated for the play behavior of young mammals. They range from general neuromuscular and cardiovascular exercise, to sensory stimulation of the developing nervous system, to learning about the environment, and to development of social, reproductive, and maternal skills. About 30 such functions have been attributed to play and exploration (*3*).

The energy budget of the young animal covers expenditures for maintenance (food getting, shelter seeking, predator avoidance, and thermoregulation), growth, and play behavior (*4*). Primates play less during periods of food shortage. Rhesus monkeys (*Macaca mulatta*) on Cayo Santiago Island played 17 times less during a 15-day food shortage. All behaviors except foraging decreased in frequency, and six of the 69 animals died, indicating the severity of the lack of food (*5*). No play occurred in two troops of 23 and 27 squirrel monkeys (*Saimiri*) in a southwestern Panama forest during 261 hours of observation. There was little of the monkeys' preferred foods available, and foraging took up 95 percent of their waking time. During the remaining 5 percent of the time, there were many social situations that in other squirrel monkey populations would have led to social play (*6*). Captive squirrel monkeys forced to obtain powdered food out of a container played as little as 1 percent of normal (*7*). There was, however, no complete cessation of play. When their food ration was