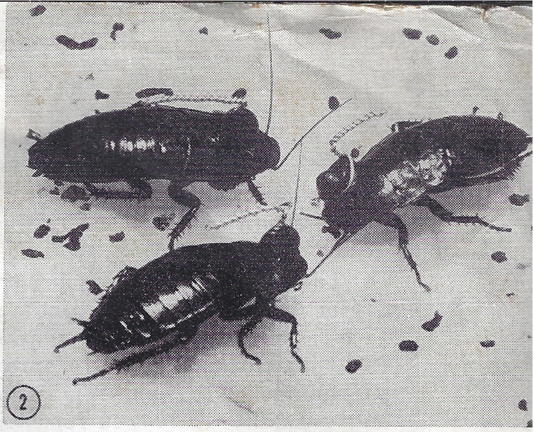

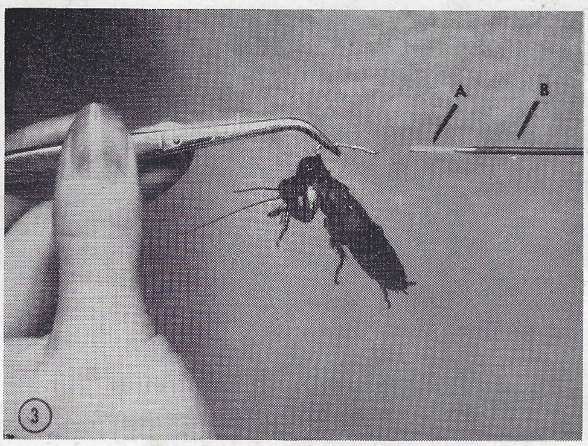

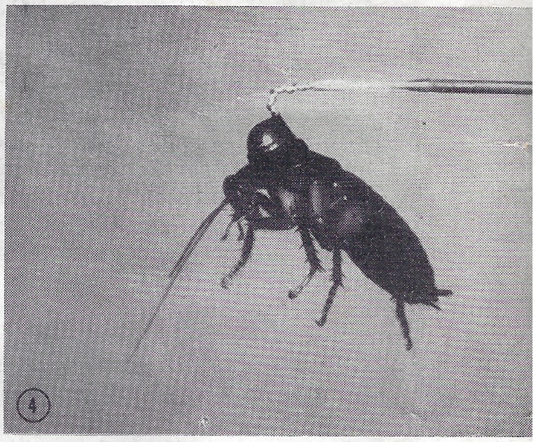

Fig. 1—Adults of the three species of roaches studied (left to right): **Diploptera punctata, Neostylopyga rhombifolia, Eurycotis floridana. Fig. 2**—Three **Eurycotis,** showing the metal handles used to seize them. **Fig. 3**—A **Eurycotis,** held by its handle, in the process of being attached to a brass rod (B). Note the coupling-link of plastic tubing (A). **Fig. 4**—Same roach as in fig. 3, affixed to rod.

Could this be a reason for resistance;
A new source for insect repellents?

Defense Sprays of Roaches

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ENTOMOLOGISTS have been familiar for many years with the remarkable ability possessed by certain insects and other terrestrial arthropods to eject a secretory spray, sometimes to a distance of several feet. The secretions frequently have a strong and characteristic odor, and their irritating properties have on occasion been the source of considerable annoyance and pain, especially to an unfortunate collector who inadvertently gets sprayed in his eyes.

The fact that these animals eject their spray only when prodded, handled, or otherwise disturbed, has given rise to the widespread belief that the sprays serve as means of defense against enemy predators. The crucial evidence in support of this contention, however, seemed to be missing, since actual predator attacks had only rarely been witnessed. This recently prompted us to do some simple experiments designed to demonstrate just how effective the sprays really are.

Study 3 Roach Species

We had available for study at our laboratory a large variety of spraying arthropods, including daddy-long-legs, millepedes, beetles, ants, earwigs, walking-sticks, grasshoppers, and cockroaches. We will restrict our comments here almost exclusively to the work done on three species of cockroaches (see fig. 1): *Diploptera punctata* (Eschscholtz), *Eurycotis floridana* (Walker), and *Neostylopyga rhombifolia* (Stoll).

Some work had already been done on these roaches in other laboratories, and much had been learned about the structure of the glands and the chemistry of their secretions. There remained unknown, however, some basic facts about the spray mechanisms themselves. How and in response to what kinds of disturbance is the spray ejected? What is its direction, range, and degree of dispersion? Answers to these questions seemed indispensable if one was to appreciate fully the effective potential of the sprays. A search for these answers became our first concern.

Two Problems at Onset

Two difficulties soon became apparent. First, since the sprays are usually imperceptible, except by their odor, a means had to be found for rendering them visible. This became possible by using special indicator papers impregnated with specific chemicals that discolored in the presence of the secretions. When a roach sprayed on a sheet of such indicator paper, the pattern of the discharge became clearly outlined.

The second difficulty stemmed from the fact that it is virtually impossible to handle the roaches without causing them to spray. Upon removal from their cages, they usually discharged repeatedly, often exhausting their secretory supply completely before one could transfer them to the indicator paper. To overcome this difficulty, we outfitted each roach with a small handle, consisting of an aluminum hook glued to the thorax just behind the head (fig. 2). Seized by this handle they could be moved about readily without ever being induced to spray.

For the experiments themselves it became necessary to prevent the roaches from moving freely over the indicator paper. To this end, each was attached to a firm brass rod. This was done simply by joining their thoracic hooks to the ends of the rods, using small coupling links of plastic tubing (figs. 3 and 4). The rods were held by universal-joint clamps, allowing the roaches to be adjusted to assume normal stances on the indicator paper. They remained linked to the rods only for as long as an experiment lasted. When it was over, the hooks were uncoupled from the rods, and the roaches returned to their cages, to be used again whenever needed.

When Will A Roach Spray?

In order to find out what specific conditions normally elicit a discharge, individual roaches, affixed to rods and placed on indicator paper, were subjected to a variety of traumatic stimuli. Appendages were lightly pinched with fine forceps, or different parts of the body were poked, tapped, or otherwise subjected to mechanical disturbance. Such stimuli invariably made them spray.

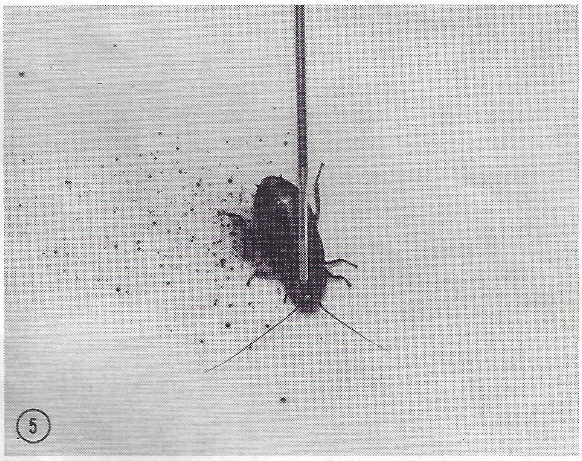
As figures 5, 6, 8, 9 clearly show, the spray patterns are by no means alike in all three species. That of *Diploptera* is much more broadly dispersed than is that of the other two. Also, *Eurycotis* and *Neostylopyga* can spray to a much greater distance than can *Diploptera*. Although our figures don't show this, we have had *Eurycotis* spray as far as three feet!

Controlled "Aim"

An unexpected additional finding was the fact that the animals can control to some extent the direction in which the spray is ejected. In *Diploptera* there are two glands, appearing on opposite sides of the abdomen, just behind the thorax. As seen in figs. 5 and 6 only that gland corresponding to the side of the body subjected to stimulation discharged at any one time. Sometimes, under special circumstances, both glands discharged synchronously. This occurred, for instance, when appendages of opposite sides were pinched simultaneously, or when a roach was persistently stimulated over its entire body surface.

Unlike *Diploptera*, *Eurycotis* and *Neostylopyga* have just a single gland, opening on the underside of the posterior half of the abdomen. The spray is invariably ejected posteriorly, but not always in exactly the same direction. By turning the abdomen to the right or to the left, they can aim with some degree of accuracy in the general direction of the stimulus (figs. 8, 9).

Certain insects other than these cockroaches can aim with much greater precision. The so called "bombardier beetles" of the genus *Brachynus* are a case in point (fig. 11). In aiming, a bombardier revolves the end of the abdomen in such a way that the tip, bearing the glandular openings, is brought to point precisely toward the stimulus. By way of



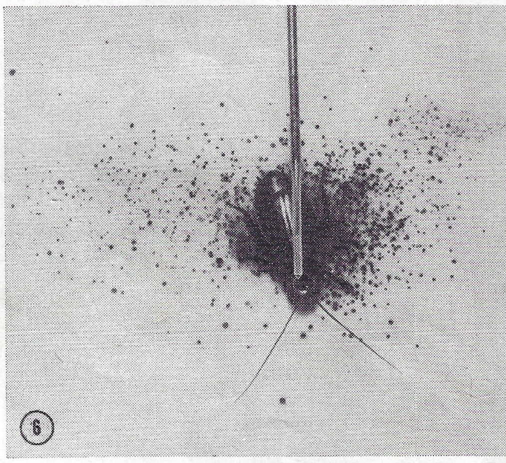
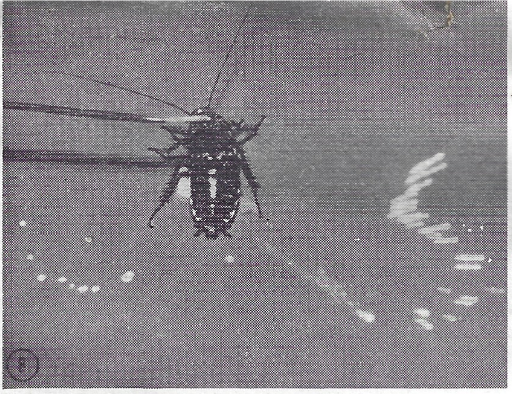
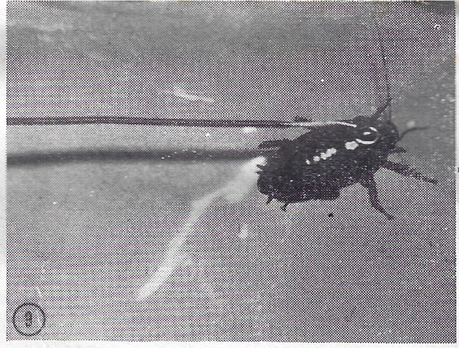
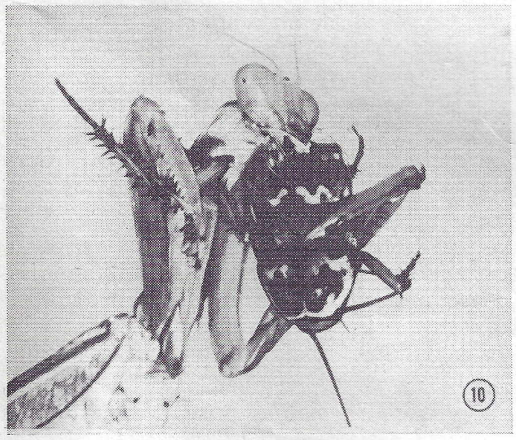


Fig. 5 — **Diploptera**: spray pattern on indicator paper following discharge of right gland in response to pinching of leg on right side. **Fig. 6** — **Diploptera**: same roach as preceding, after having sprayed a second time, but now from the left gland following pinching of leg on left side. **Fig. 7** — Two **Diploptera** exposed to attack by ants. The one on left has had its glands operated out, and is under persistent attack. The one on right was attacked, but sprayed, and repelled its assailants.







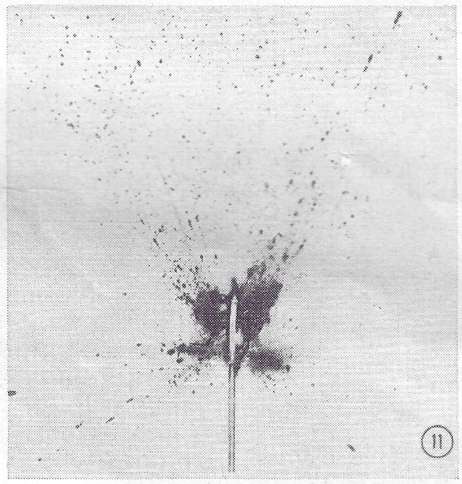


Fig. 8 — Neostylopyga: spray patterns of two consecutive discharges. The discharge on left followed pinching of left hind leg. That on right followed pinching of the corresponding leg on the right side. **Fig. 9 — Eurycotis:** spray patterns of two consecutive discharges elicited by pinching right and left hind legs, one at a time, as in **Neostylopyga** of fig. 8. **Fig. 10** — A praying mantid in the process of devouring a **Neostylopyga.** Mantids were never repelled by this roach. **Fig. 11** — A bombardier beetle after having discharged four times. The discharges were evoked by pinching in succession each of the front and hind legs. Note that every discharge is accurately aimed toward the particular appendage stimulated.

this turret-like arrangement, it can direct the spray accurately in almost every direction. Some earwigs and walking-sticks that we have been working with are capable of equally outstanding marksmanship.

The mechanisms by which the different glands operate are interesting in themselves. In some cases we do not know exactly what the mechanism is, although safe inferences can usually be made from the anatomical details of the glands. In *Diploptera* and *Eurycotis*, the glands have been admirably described in recent papers by Dr. L. M. Roth and Dr. B. Stay of the Army Quartermaster Corps., in Natick, Mass. Those of *Diploptera* appear to function somewhat like commercial atomizers. Each gland features a relatively capacious sac-like reservoir in which the secretion is stored. This reservoir leads directly to the outside, opening through a small valve-like orifice. Internally, the reservoir does not end blindly, but leads by way of a narrow connection to the internal air-tubes of the respiratory system of the insect. Ejection of the spray is presumably accomplished by forcing the air from the respiratory tubes into the reservoirs, thereby expelling and dispersing the secretion.

The single glands of *Eurycotis* and *Neostylopyga* are much less elaborate in structure. They too feature a reservoir, but in their case it is a blind sac, having no connection with the respiratory air tubes. Ejection of the secretion is apparently brought about by the contraction of special muscles that insert on the walls of the reservoir, and by the simultaneous compression of the abdomen.

Repellent Action Varies

There remained to be seen what effects, if any, the sprays had on potential enemy predators. We constructed special arenas, consisting of glass enclosures lined with indicator paper, into which individual roaches were released, together with the particular predator to be tested. Among the predators that we tried were ants, carabid beetles, praying mantids, spiders, frogs, lizards, and birds.

On the whole, the sprays proved to be tremendously effective. *Diploptera*, for example, instantly repelled most of the ants, carabids, and spiders (fig. 7). All of these predators attacked readily, each in its own characteristic way. Ants and carabids usually seized individual appendages, while spiders pounced directly upon the body itself, attempting to grasp it with their sharp chelicerae. This invariably elicited a spray ejection. As was to be expected, the discharge was always unilateral in those cases where just one side of the body had been traumatized. Hit by the spray, the assailants retreated instantly, sometimes leaving a conspicuous dark streak on the indicator paper from secretion trailing from their bodies. In most cases the roaches betrayed no signs of injury after such an attack. The predators, on the other hand, often showed conspicuous behavioral abnormalities, undoubtedly attributable to the toxicity of the secretion. The ants and beetles, for instance, had peculiar seizures, during which leg movement became completely discoordinated, and locomotion strongly impaired. Interestingly, the seizures never lasted for more than a few minutes, and were always followed by complete recovery.

Diploptera also proved quite effective in repelling frogs. Typically, a frog would leap at a roach, seize it, and then jump back instantly, spitting it out again. The roach, unhurt, would flee unmolested, leaving the frog lingering on its belly for a few seconds, open-mouthed and "pawing" its tongue.

Eurycotis and *Neostylopyga* also repelled some of the smaller arthropod predators, but somewhat less effectively than did *Diploptera*. Larger predators such as birds, lizards and frogs were also usually repelled, the effect being especially dramatic in cases where some secretion had hit the eyes. A blue jay, after having received the full impact of a *Eurycotis* discharge, was seen to maintain one eye closed for a full ten minutes following the encounter. Similarly, a lizard, after making a "pass" at a *Neostylopyga,* dug its head in the sand, and rubbed it back and forth in obvious discomfort. We ourselves have been sprayed in the eyes and can attest to the sharp pain that this entails.

Not all results were as clear cut as these. Certain lizards were found to eat *Diploptera* readily, suffering no immediate aftereffects. Yet, after eating these roaches for a few days, the lizards began ignoring them, shifting their attention instead to a more palatable insect, introduced as a choice at that time.

Other predators seemed to be completely unaffected by the sprays. Praying mantids for instance ate *Diploptera* and *Neostylopyga* when these were offered to them for the first time, and continued eating them indefinitely, without ill-effects, and without developing any long-term discriminatory tendencies against them (fig. 10).

The fact that these roaches differ somewhat in the effectiveness with which they repel the various predators is not surprising, since they do not secrete the same chemicals. Roth and his collaborators at Natick have identified the active principles of the secretions of *Diploptera* and *Eurycotis.* *Diploptera* secretes a mixture of quinones (*p*-benzoquinone, and two of its derivatives), whereas *Eurycotis* secretes an aldehyde (2-hexenal). The secretion of *Neostylopyga* has not yet been analyzed, but it is unquestionably distinct from that of the other two (It's odor, for one thing, is completely different).

A great deal is being done in several laboratories throughout the world on the chemical defense mechanisms of insects and other arthropods. Many of the active principles of the secretions have already been analyzed, and attempts are being made to evaluate their specific functions. Some of this work may ultimately be of practical value, inasmuch as it may provide clues as to what specific chemicals might be worth investigating in connection with the formulation of new or improved commercial repellents. In addition, some of the secretions have been found to possess rather powerful antibacterial action, a circumstance that is encouraging some laboratories to investigate their potential usefulness as medical antibiotics.

Basically, however, the main value of this research lies in its purely biological implications. It is clarifying some fundamental aspects of predator-prey relationships, and is therefore contributing to our understanding of biological competition in general. One of the conspicuous features of the present day land fauna is the evolutionary supremacy of arthropods, and of insects in particular. One cannot help but wonder whether the achievement of dominance was attributable to a significant extent to the possession of effective means of chemical defense. The widespread occurrence of these defense mechanisms would appear to lend at least some support to this contention. It is certainly an odd fact (and, one might add, a heartening one—at least to those of us whose interest in insects stems entirely from their suitability for biological research) that insects should have evolved a successful spray program all of their own, long before man first conceived of developing a counterpart.

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