# DEFENSIVE SPRAY MECHANISM OF A SILPHID BEETLE *(NECRODES SURINAMENSIS)**

BY THOMAS EISNER AND JERROLD MEINWALD
Section of Neurobiology and Behavior,
and Department of Chemistry,
Cornell University, Ithaca, NY 14853

## INTRODUCTION

Although much has been learned about chemical defenses of beetles in recent years (Weatherston and Percy, 1978), few studies have been made of Silphidae, the family that includes the largest carrion beetles. As is known to anyone who has collected these insects, many silphids respond to disturbance by emitting a nauseatingly malodorous ooze from the anus. The fluid is said to be strongly alkaline in some species, and rich in ammonia (Schildknecht and Weis, 1962). In *Silpha,* a gland had been noted that opens into the rectum (Dufour, 1826; Leydig, 1859), but no chemical work had been done to determine whether specific defensive chemicals in the anal effluent might stem from the gland.

Personal observation had told us that one silphid, the so-called red-lined carrion beetle, *Necrodes surinamensis,* might be unusual. First, the beetle seemed able to eject its anal fluid as a spray rather than an ooze, which no other silphid had been reported to do, and second, the fluid gave an acidic test on indicator paper and had a stench that was overlain by a distinct aromatic fragrance.

We have now studied *N. surinamensis* in some detail. Chemical work, carried out in collaboration with others, led to the isolation of several fatty acids and terpenoid compounds, present in the spray and produced by a special rectal gland. An account of these chemical findings, which are summarized in Figure 1, will be published elsewhere. We here give details of the beetle's defensive behavior, plus a brief description of the gland, and data on the beetle's unacceptability to predators.

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## Procedures and Results

*Necrodes surinamensis* is a large beetle, about 2 cm in average body length. It occurs throughout the United States, east of the Rocky Mountains. It is mostly taken at carcasses. We collected large numbers at baits (dead fish and chickens) in the environs of Ithaca, New York, and on the grounds of the Archbold Biological Station, Lake Placid, Florida. They were maintained in the laboratory on commercial meat-based dog food preparations. Observations were made mostly on freshly captured specimens.

Spray ejection was studied by techniques previously used with other chemically protected arthropods (Eisner, 1958). The beetles were individually fastened with wax to tethers and placed in normal stance upon sheets of indicator paper (filter paper presoaked in red alkaline phenolphthalein solution, blotted off to near dryness just before use). They were then subjected to simulated attack by pinching some of their appendages with forceps or briefly touching parts of the body with a hot spatula. Their responses were immediate. No sooner had a stimulus been applied than they revolved the abdominal tip, which projects free beyond the posterior margin of the elytra, aimed it toward the site stimulated, and sprayed. As evidenced by the pattern of white spots induced by the acid fluid on the indicator paper, the discharges were accurately directed (Fig. 2A, B). The site of emission of the spray was clearly noted to be the anus. The abdominal tip is essentially a revolvable emplacement for the anal nozzle. It can be pointed in all directions, even anteriorly over the beetle's own back (Fig. 2C–F). Regions of the body stimulated were always noticeably wetted by the spray. Beetles that had remained undisturbed in confinement for several days, and were tethered without being caused to discharge (they were kept refrigerated during the tethering procedure), proved capable of spraying repeatedly, even in quick succession if a rapid sequence of stimuli was applied. The number of discharges ($\bar{x} \pm$ sd) that could be elicited from such beetles was $4.9 \pm 1.1$ (N = 5 females + 3 males). Only direct contact elicited discharges. The beetles never sprayed in response to movement or tapping nearby.

The rectal gland, which is identical in both sexes, was readily exposed by dissection. It consists of a tubule and a sac (Fig. 3). The tubule lies free in the hemocoel, is long and narrow (actual measurement in a female = $18 \times 0.2$ mm) and closed at its distal end. It opens proximally into the bladder-like sac, which itself opens by

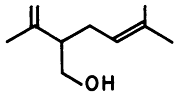
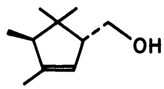
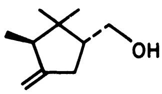
| Aliphatic Acids | | µg per Beetle |
|---|---|---|
| Caprylic acid | $CH_3(CH_2)_6CO_2H$ | 25 |
| Capric acid | $CH_3(CH_2)_8CO_2H$ | 5 |
| *cis*-3-Decenoic acid | $CH_3(CH_2)_5CH{=}CHCH_2CO_2H$ | 5 |
| *cis*-4-Decenoic acid | $CH_3(CH_2)_4CH{=}CH(CH_2)_2CO_2H$ | 5 |
| **Terpene Alcohols** | | |
| Lavandulol |  | 4 |
| α-Necrodol |  | 14 |
| β-Necrodol |  | 3 |

Fig. 1. Substances isolated and characterized from the rectal gland of *Necrodes surinamensis*. The two terpene alcohols, α-necrodol and β-necrodol, are new natural products; *cis*-3-decenoic acid and *cis*-4-decenoic acid have not previously been reported from an insectan source. Details of the chemical procedures will be published elsewhere.

way of a narrow neck into the rectum. The tubule is surrounded by a loose meshwork of muscle fibers, clearly identifiable as such in whole mounts of the gland viewed by transmitted polarized light. Comparable compressor muscles, arranged in a thick layer, envelop the sac. The entire gland has an inner lining of membranous cuticle, which was readily isolated by treatment of the gland with 10% aqueous potassium hydroxide, and was shown to be continuous with the cuticular lining of the hindgut. In freshly dissected preparations, both parts of the gland were seen to be filled with clear fluid. The hindgut, in contrast, was usually replete with opaque fecal paste.

The compounds listed in Figure 1 had been shown to be present both in extracts of isolated glands and in samples of the spray itself. None were present in more than trace amounts in extracts of the region of the hindgut anterior to the glandular junction. It seemed reasonably certain, therefore, that the fatty acids and terpenes are products of the gland rather than the enteron. This conclusion was further supported by circumstantial evidence. Fluid squeezings from isolated glands, unlike squeezings from the hindgut, gave acidic spot

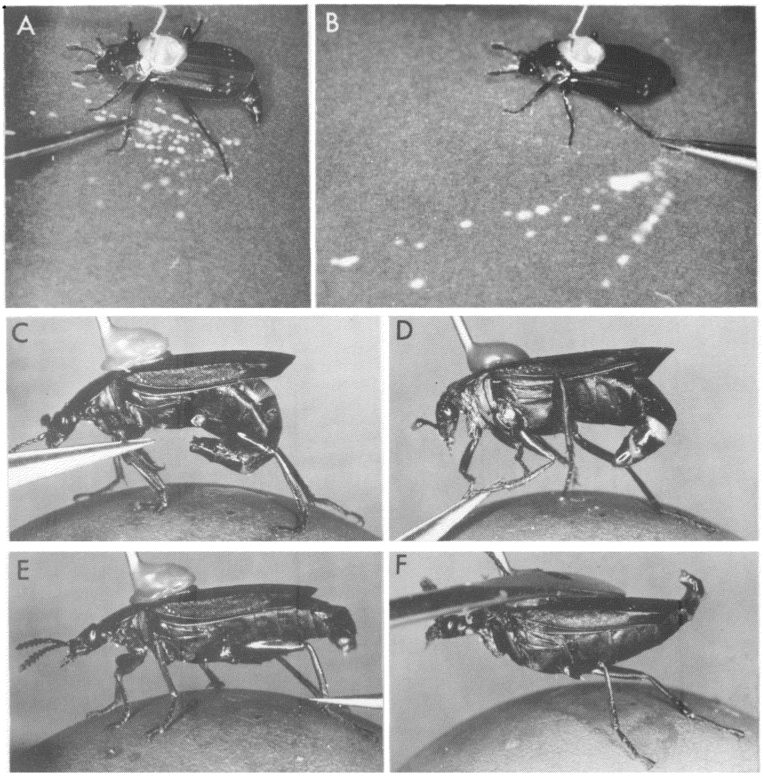



Fig. 2. A–B, Aimed discharges elicited by pinching a left midleg (A) and left hindleg (B) of *Necrodes* with forceps. The spray pattern is visible on phenophthalein indicator paper. C–F, Directional aiming movements of the anal turret of *Necrodes*. Note that the abdominal tip is accurately pointed toward the site of application of the stimulus: (C) tibia of midleg, (D) tarsus of midleg, (E) tibia of hindleg, pinched with forceps; (F) back of beetle touched with hot spatula.

tests on phenolphthalein indicator paper and had the recognizable terpenoid fragrance of the spray.

Examination of fresh spray ejected by *Necrodes* on glass showed occasional presence of opaque material in the discharged fluid, suggesting that the secretion may sometimes be expelled with admixture of fecal paste. Since the glandular contents are forced to the outside by way of the rectum, such admixture may occur whenever the pathway of secretory egress is blocked by enteric matter. Two fatty acids not listed in Table 1, stearic acid and palmitic acid, were

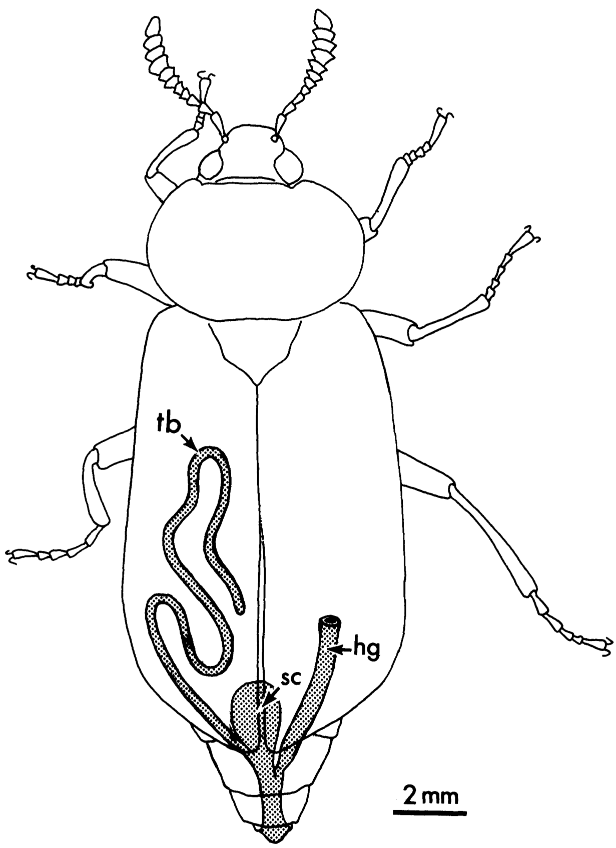



Fig. 3. Diagram of *Necrodes surinamensis* showing the position of the rectal gland (tb = tubule; sc = sac) relative to the hindgut (hg).

identified as occasionally present in the spray. Neither was detected with consistency or in substantial amounts in extracts of the gland, but they were always present in extracts of the hindgut. Their occurence in the spray may be a further indication that rectal contents are sometimes ejected with the secretion.

Laboratory tests done with formicine ants *(Formica exsectoides)* and Swainson's thrushes *(Catharus ustulatus)* demonstrated that *Necrodes* is well protected against such predators. The tests with *Formica* involved presenting individual tethered *Necrodes* to groups of 10 ants in small glass enclosures. The ants attacked immediately, by clamping onto the beetles with their mandibles, in response to which the beetles revolved their abdominal tip and sprayed. As was particularly clear from the patterns of droplets sometimes visible on the bottom of the enclosures, the discharges were accurately aimed toward the ants. These usually released their hold quickly and fled. At varying intervals thereafter they engaged in intensive cleansing activities, which seemed all the more protracted when the ants had been heavily contaminated with spray. Five beetles were exposed to ants in this fashion for 30 min. each. None received noticeable injury.

The tests with the thrushes followed a protocol previously used with these birds in experiments with other chemically protected insects (Eisner *et al.,* 1978). *Necrodes* were offered together with mealworms (larvae of *Tenebrio molitor,* which served as edible controls) to 3 individually caged birds (all males), in 3 daily feeding sessions per bird. Mealworms outnumbered *Necrodes* 2 to 1. The insects were offered one at a time, up to a total of 14–15 per session. Sequence of presentation was such that each series of 3 consecutive items consisted of two mealworms and one randomly placed *Necrodes.* Each item was left with a bird until it was eaten, or for a maximum of 2 min. Fate of prey was scored as follows: eaten (*E*, if the insect was ingested after having been pecked no more than 3 times); eaten with hesitation (*EH,* if the insect was eaten after having been pecked more than 3 times); rejected (*R*, if the insect was ignored after having been pecked one or more times); not touched (*NT*, if the insect was not contacted by the bird during the 2 min. of presentation). Insects not touched at the end of a feeding session were not tallied, since such avoidance might have been due to satiation of the bird.

The results, lumped for the 9 feeding sessions with the 3 thrushes, are shown in Figure 4. It is clear that the birds rated *Necrodes* distinctly undesirable relative to mealworms. While the latter were all eaten outright, 74% of *Necrodes* were either rejected or left untouched. The 26% that were eaten were only taken after repeated peckings. A special point was made to check the rejected *Necrodes* for injury. None was found to bear any, and all were live when examined several days later. Although it proved impossible to determine with certainty whether *Necrodes* always sprayed when pecked or grasped by a bird, in some cases there was evidence that discharges had occurred. Streaks of spray occasionally made their appearance on the glossy floor of the cage during an attack, or birds shook their heads violently after seizing a beetle, as we have repeatedly seen captive thrushes do when attempting to take insects that spray (e.g. carabid beetles).

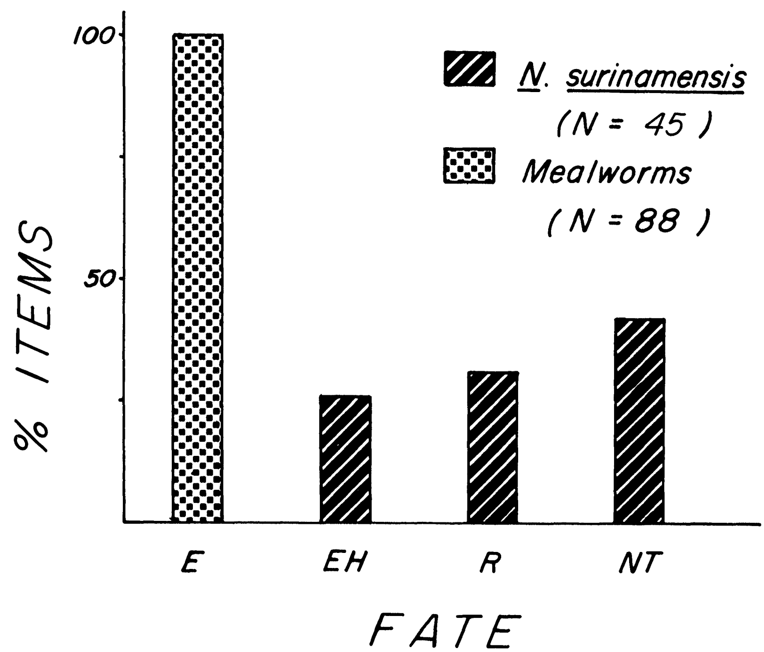



Fig. 4. Fate of *Necrodes surinamensis* and mealworms fed to three Swainson's thrushes; *E* = eaten; *EH* = eaten with hesitation; *R* = rejected; *NT* = not touched. Details in text.

## Discussion

The discovery of a chemical defense mechanism in an insect should come as no surprise, since such mechanisms are extraordinarily widespread among arthropods. Moreover, many insects, including a multiplicity of beetles, termites, ants, earwigs, caterpillars, and phasmids, eject their defensive secretions in the form of accurately directed jets. *Necrodes* is anomalous in that it expels its aimed secretory discharges from the anus. Other beetles that spray, such as Carabidae, also discharge from the tip of the abdomen and may aim their ejections by movement of the abdominal tip (e.g. Eisner, 1958), but their glands are integumental and open beside the anus on the body wall itself. *Necrodes* is further unusual in that it has only one gland. Exocrine defensive glands in beetles commonly occur in pairs.

It seems reasonable to presume that the gland of *Necrodes* arises developmentally as an outpocketing of the rectum. Other rectal glands in Silphidae, such as that of *Silpha,* are doubtless homologous to that of *Necrodes.* We feel this to be so despite some differences in gland morphology [In *Silpha americana* the lateral tubule is reduced to a short elaborately subdivided diverticulum (Alsop, 1970)]* and in gland chemistry (*Silpha americana,* as we shall report elsewhere, produces steroids in its gland). While in the absence of histological work little can be said about the function of the two parts of the *Necrodes* gland, the strongly muscled condition of the sac suggests that it might serve as the reservoir from which secretion is expelled for the discharge. The tubule might be strictly secretory.

It seems clear from the tests with ants and birds that *Necrodes* is relatively unacceptable to such predators. But to what extent this is attributable to the glandular components of the spray, or to enteric additives of the spray, or even to entirely different factors (carrion contamination of the beetle's body?) remains to be seen. The secretion, no doubt, plays a defensive role, but the other factors may amplify the effect. It is interesting in this connection that another common inhabitant of carrion, the staphylinid beetle *Creophilus*

*Dufour (1826) writing of *Silpha littoralis,* speaks of a rectal gland with a "vaisseau sécréteur" almost as long as the body, suggesting that he was dealing with a gland similar to that of *Necrodes.*

*maxillosus,* also mixes intestinal fluid with the secretion of its defensive glands (Jefson *et al.,* 1983). A diet of carrion, one might imagine, could render an insect's enteric contents potently deterrent. The ammonia reportedly present at high concentrations in the anal effluent of some silphids (Schildknecht and Weis, 1962) is probably derived from decaying ingested animal protein and may well serve for defense. To us at least, the odor of the intestinal fluid discharged by many carrion insects upon handling, or for that matter the odor of the insects themselves, is repugnant. The fragrance emitted by *Necrodes* after a discharge is transient, and certainly does not mask the intrinsic stench of the animal.

While it would have been desirable to test the various secretory components of *Necrodes* for repellency, this proved impossible due to lack of sufficient synthetic quantity of $\alpha$-necrodol and $\beta$-necrodol, the two most interesting novel compounds in the mixture. It seems likely, however, that these terpenes are deterrent to insects. They are cyclopentanoid compounds, of which many are known to occur in the defensive glands of insects and in plants (Nakanishi *et al.,* 1974), and some are provenly repellent to insects (Eisner, 1964; Smolanoff *et al.,* 1975; Meinwald *et al.,* 1977; Jefson *et al.,* 1983). Fatty acids have also been reported from other arthropodan defensive glands. They may themselves be deterrent, and may also serve as surfactants. As part of a spray they may promote spread and penetration of droplets on target, a role that has been demonstrated for caprylic acid in whip scorpion secretion (Eisner *et al.,* 1961). The fatty acids of *Necrodes* may have a similar function, and may also facilitate the mixing of the apolar glandular material with the largely aqueous enteric fluid when the two are discharged together. Two of the *Necrodes* fatty acids, *cis*-3-decenoic acid and *cis*-4-decenoic acid, have not previously been identified from an insectan source. The apparent enteric, rather than glandular, origin of stearic and palmitic acid should come as no surprise, since these fatty acids are major components of animal fats and hence likely to be ingested by *Necrodes* with carrion.

Only speculation can be offered to account for the presence of lavandulol in the *Necrodes* spray. The substance has not previously been reported from insects, although it is known from plants as a major component of lavender oil (Karrer, 1958). We suspect the compound to be repellent to insects, as some low molecular terpenes are known to be, which if true would provide some explanation for the presence of the substance in plants. An increasing number of compounds known previously only from plants is being isolated from the defensive glands of insects. In our judgment the very occurrence of such compounds as defensive agents in animals suggests that they may (sometimes at least) fulfill a similar function in plants.

Carrion insects, often crowded in their food source, undoubtedly interact in subtle competitive ways. To what extent *Necrodes,* or for that matter any other chemically protected carrion insect, makes use of its defensive glands in such interactions, remains an intriguing unknown.

## Summary

When disturbed, the carrion beetle *Necrodes surinamensis* (family Silphidae) ejects jets of fluid from the anus. The abdominal tip, which projects beyond the posterior margins of the elytra, serves as the revolvable turret by which the ejections are aimed. Only contact stimulation elicits discharges. The fluid is primarily of glandular origin but may contain admixed enteric matter. The gland, which consists of a tubular portion and a vesicular sac, opens into the rectum itself. Chemical work (to be reported elsewhere) has shown the secretion to contain two novel cyclopentanoid compounds ($\alpha$-necrodol and $\beta$-necrodol) as well as lavandulol and several fatty acids. Two of the fatty acids, *cis*-3-decenoic acid and *cis*-4-decenoic acid, were not previously known from insects.

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