prior drug history can influence a drug's behavioral effect and can also determine whether that drug will maintain responding that results in its administration. The likelihood that certain compounds will be abused may be modified by factors other than the pharmacological properties of the drug. Such experimental evidence now suggests that conditions that have existed in the past, as well as conditions in the current environment can play a significant role in determining the behavioral effects of a wide variety of drugs. A focus on these variables may aid in understanding and clarifying basic behavioral and psychopharmacological principles of drug abuse.

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# **Defense in Thrips: Forbidding Fruitiness of a Lactone**

Abstract. Expulsion of anal fluid from the upturned abdomen was demonstrated to serve a defensive function in the thrips Bagnalliella yuccae. An allomone in the anal exudate was identified as  $\gamma$ -decalactone, a fruity-smelling compound that repelled potential predators. Chemical defenses may contribute to the ability of thrips to maintain large aggregations.

The Thysanoptera (thrips) (1) include some 6000 described species, many of which are of economic significance (2). Understanding of the chemical ecology of thrips is limited, probably as a result of their small size (many species measure about 1 mm) and cryptic nature. A number of species form aggregations that can be easily detected by predators. Although it has not been shown that such assemblages of thrips are chemically protected, many species raise their elongate abdomens when disturbed, with

some exuding odoriferous fecal droplets (3). We report that the fruity-smelling component of the anal exudate of the gregarious thrips Bagnalliella yuccae is  $\gamma$ -decalactone, a compound that effectively repels small predators such as ants.

Bagnalliella yuccae live in aggregations between the closely appressed leaf bases of its host Yucca filamentosa (bear grass). The plant provides two types of protection: (i) many small predators are excluded by the tight confines between

leaves, and (ii) the radiating, needlepointed leaves deter large herbivores that might otherwise consume the thrips along with the leaves.

Thrips-infested Yucca leaves collected from Athens, Georgia, were sandwiched between panels of glass and placed under a dissecting microscope. The disturbed insects were allowed 24 hours to reassemble and then were challenged by the introduction of workers of Monomorium minimum, a predatory ant found on Yucca plants (4). Being slightly larger than their prey, the foraging ants were not always able to breach the narrow crevices protecting the thrips. However, when attacks occurred, thrips flexed the tip of the abdomen toward the assailant while exuding a droplet of anal fluid (Fig. 1A). When disturbed, thrips often held the abdomen aloft for several seconds (Fig. 1B), sometimes supporting a droplet of the clear, peachy-smelling anal fluid. From this position, frontal as well as broadside attacks could be rapidly countered with the turret-like abdominal tube. The tube is effective as a liquid applicator since its tip bears elongate setae that form a paintbrush for the exudate (Fig. 1C).

Ants contacting the exudate quickly withdrew, wiping exposed body parts on the substrate and displaying other grooming behaviors. The fluid also seemed to have an indirect effect: untouched ants avoided the vicinity in which the exudate had been released. Under these laboratory conditions, pursuing ants did not subdue adult thrips, although occasionally a few sluggish larvae were captured (5).

A preliminary test established that the thrips' discharge can repel predators. Glass tubes with cotton plugs at one end were streaked inside with exudates of thrips or were left empty (controls). The tendency of M. minimum workers from laboratory colonies to explore the tubes was compared (6). During 15 minutes, a mean  $\pm$  standard deviation (S.D.) of only  $1.6 \pm 2.6$  workers entered the exu-

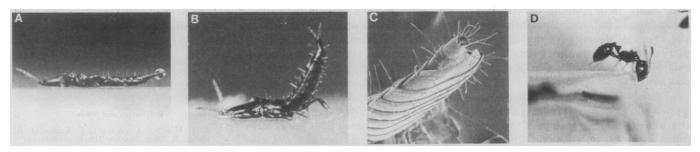


Fig. 1. (A) An unusually large anal droplet held by an adult B. yuccae. (B) Typical defensive posture. (C) Turret-like abdominal tube at the tip of the upraised abdomen ( $\times$  100). (D) Monomorium minimum worker with antennae deflected, standing above opening of a tube containing  $\gamma$ -decalactone.

date-treated tubes, significantly fewer (P < .05, Wilcoxon test) than the 42.0  $\pm$  17.6 ants visiting the empty tubes.

Gas chromatography of whole body extracts revealed a single major volatile component in B. yuccae (7). Its mass spectrum contained a minor parent ion at a mass-to-charge ratio of 170, important ions at 152, 141, and 128, and a base peak at 85, identical to the published spectrum for  $\gamma$ -decalactone (8). An authentic sample of this lactone (9) had an identical retention time and mass spectrum and also had a fruity odor similar to that of the exudate from the thrips. The compound was easily identified in extracts of the anal exudate and was concentrated in the hindgut (10). Adults contained approximately twice as much lactone as larvae  $[0.27 \pm 0.15 \text{ (S.D.)} \text{ versus } 0.12$  $\pm$  0.10 µg, respectively] (11). The lactone could not be detected in leaves of the host plant (12).

The repellency of  $\gamma$ -decalactone was determined with predatory ants in both the laboratory and field. Glass tubes were prepared as before and treated with ethanol solutions of the synthetic compound or with ethanol alone (control) (13). In tests on laboratory colonies of M. minimum, the number of workers entering the tubes decreased as the concentration of lactone increased, approximately two thrips equivalents evoking 50 percent repellency (13). Similar results were obtained in laboratory tests with two other predatory ant species, M. pharaonis and Iridomyrmex humilis. In the field, a modified test on foraging M. minimum workers corroborated our laboratory findings (14). A mean  $\pm$  S.D. of  $1.3 \pm 1.5$  workers entered tubes streaked with ten thrips equivalents of  $\gamma$ decalactone, while  $13.0 \pm 4.4$  ants visited the control tubes (P < .05, Wilcoxon test). In further evidence of the offensive nature of the chemical, ants feeding at the mouth of control tubes often directed their antennae toward their food but those feeding at treated tubes deflected their antennae (Fig. 1D).

These results indicate that the defensive ability of *B. yuccae* depends on protective habitat, defensive behavior, and chemical assault. Among aggregative species of thrips, communal living may provide the advantage of a shared pool of defensive resources.

 $\gamma$ -Decalactone has been isolated from a yeast and from dairy products and is a constituent of the aroma of several fruits, including peaches and strawberries (15). There are no published accounts of its occurrence in animals (16), but our inability to detect the compound in the leaves of *Yucca filamentosa* indicates that it is not of dietary origin.

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   Glass bridges permitted ants from laboratory
- colories to reach the thrips.
   Of 40 encounters, 26 ended when an adult thrips
- 5. Of 40 encounters, 26 ended when an adult thrips raised its abdominal tube or daubed the ant with fluid (or both), and 14 ended when an adult escaped by walking away or remained motionless until the inspecting ant departed. Larval encounters were not counted.
- 6. A 5-mm cotton plug was placed in one end of a tube (length, 3.75 cm; inner diameter, 0.5 cm). Twenty-five adult thrips were gently held (with watchmaker forceps) against the tube's interior as they exuded fluid. Six tubes were prepared in this way. One tube containing exudate and one empty tube were placed in the foraging arena of each of six ant colonies. Ants inside each tube were counted at 1, 5, 10, and 15 minutes.
- Methylene chloride extracts were analyzed by gas chromatography (LKB 2091 instrument); the column (2.0 m by 2.0 mm) was packed with 1 percent SP-1000 and was programmed to increase in temperature from 50° to 250°C at 8° per minute
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- Gas chromatography indicated that γ-decalactone constituted more than 99 percent of the volatile substances in a synthetic standard (Aldrich). The possible optical activity of the thrips' volatile material was not determined.
- 10. Exudates were collected with a fine capillary tube and transferred into a vial of CH<sub>2</sub>Cl<sub>2</sub>. The guit was removed from ten thrips (anesthetized under cold Ringer solution), and methylene chloride extracts were prepared from hindgut, foregut, midgut, and Malpighian tubule fractions. Gas chromatography showed the lactone in abundance only in the exudate and hindgut.
- Fifteen larvae and adults were individually crushed in a V-shaped vial and their lactone content quantified by using gas chromatography to compare CH<sub>2</sub>Cl<sub>2</sub> extracts to standards. The lactone content of adults was 6.3 μg/mg and of larvae was 3.1 μg/mg (wet weight).
- Yucca filamentosa leaves were steam-distilled into ethyl acetate, extracted with methylene chloride, and analyzed by gas chromatography.
- 13. Portions (5 µl) containing 0, 0.25, 1.0, 2.5, 10, or 25 thrips equivalents (TE) of the lactone (1 TE = 0.27 µg) were applied with a microsyringe. Tubes were allowed to dry 3 minutes before presentation to five colonies of *M. minimum*. The order of presentation of the concentrations was randomized, each colony being tested for each concentration twice (*N* = 10 tubes per concentration). Antis were monitored as before. Scores, expressed as percent of control counts, were 0.25 TE, 116 percent; 1 TE, 69 percent; 2.5 TE, 16 percent; 10 TE, 5 percent; and 25 TE, 2 percent.
- and 25 1E, 2 percent.
  14. Monomorium minimum foragers were reluctant to enter tubes in the field. Therefore, an end plug of honey was substituted for the cotton with a streak of the food drawn along the interior of the tube to entice workers. Tubes containing exudate and control tubes were placed along recruitment trails of six colonies; the number of workers inside the tubes was counted after 15 minutes.
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# Retraction of Data on the Human c-ras<sub>1</sub><sup>H</sup> Oncogene

We published a paper entitled, "The human c-ras<sub>1</sub><sup>H</sup> oncogene: A mutation in normal and neoplastic tissue from the same patient" on 18 February 1983 (1), in which we claimed to have identified, by means of the Southern blotting technique, a tumor as well as normal tissue with the  $c-ras_1^H$  oncogene mutation. In pursuit of these studies, we developed two independent lymphocyte cell lines from this patient. They were prepared by transformation with Epstein-Barr virus. These cell lines, which proved to be karyotypically normal, did not contain the mutant allele. At this point, we reevaluated our original findings and again extracted DNA from a portion of the tumor which had been frozen to repeat the analysis. The DNA from the second extraction of the tumor does not contain the  $c - ras_1^H$  oncogene mutation. We now believe that the original extractions of DNA from this patient, which were performed simultaneously, were contaminated by a plasmid DNA containing the  $c-ras_1^{H}$  oncogene and that this contamination led to spurious results.

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