



Trail Odors: Recognition by Insects Parasitic on Cocoons

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ministration of L-dopa to parkinsonian patients has been observed to cause a hypotensive response (15). It has also been pointed out by Henning (16) that the acute hypotensive effects of alpha-methyl-dopa are mediated by a central mechanism requiring the decarboxylation of this amino acid. This action might be due to the replenishment of catecholamine-deficient fibers with the alpha-methylated analogs. The hypotensive action of the monoamine oxidase inhibitors could also be rationalized by relating the buildup of central catecholamines to drug action. Catecholamine-depleting compounds such as reserpine may be hypotensive simply because they also deplete the peripheral amine stores which are required for the maintenance of the hypertensive state.

It can be concluded that catecholamine mechanisms in the central nervous system may play an important role in the regulation of blood pressure, and that genetic hypertension in the rat and possibly in man may be related to a deficiency of catecholamines in certain areas of the brain.

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Trail Odors: Recognition by Insects Parasitic on Cocoons

Abstract. Female parasitic insects in the genera *Pleolophus*, *Endasys*, and *Mastrus* (Hymenoptera: Ichneumonidae) search the ground cover for hosts and avoid areas they have already inspected. Females respond to their own trail odor, and recognition occurs also between conspecific, congeneric, and intergeneric individuals. This is the first direct evidence for recognition between parasitoids at sites other than on the host itself, and between females of different species.

Discrimination between parasitized and unparasitized hosts by parasitic insects results in the optimum survival of their progeny. The ability to discriminate has been well documented (1) and is considered to be a common attribute of parasitoids (2). Here I report observations showing that parasitoids also discriminate between presearched and unsearched areas. This is adaptive, since searching becomes more efficient when presearched areas can be avoided. Also, intraspecific recognition of trails could cause a more even dispersion of individuals throughout the habitat.

Discrimination at the site of the host can result from detection of a previous parasitoid by its odor (3). Salt (3) found

that females of *Trichogramma evanescens* could detect the odor of another female left on a host egg 2 days earlier. Discrimination also resulted when a water solution, made by washing glass over which the females had walked, was painted on a host egg. Ulyett (4) suggested that female *Bracon hebetor* retrace their trails by using olfactory stimuli. Many species of Ichneumonidae emit easily detected, pungent odors thought to be protective (5). These may also serve as the odors that other parasitoids can detect and avoid. I found that female *Pleolophus basizonus* avoided an area they had previously searched (6).

Two experiments were performed to test the ability of female parasitoids to

Table 1. Probability of parasitoids showing apparent recognition of odors in the treatment as frequently as in the control (7).

Second species present	First species present			
	<i>Pleolophus basizonus</i>	<i>Pleolophus indistinctus</i>	<i>Endasys subclavatus</i>	<i>Mastrus aciculatus</i>
<i>Pleolophus basizonus</i>	0.005*	0.025*	0.050*	0.010*
<i>Pleolophus indistinctus</i>	.750	.050*	.005*	.500
<i>Endasys subclavatus</i>	.250	.005*	.025*	.025*
<i>Mastrus aciculatus</i>	.250	.050*	.025*	.050*

* Significant difference at 5 percent level or less.

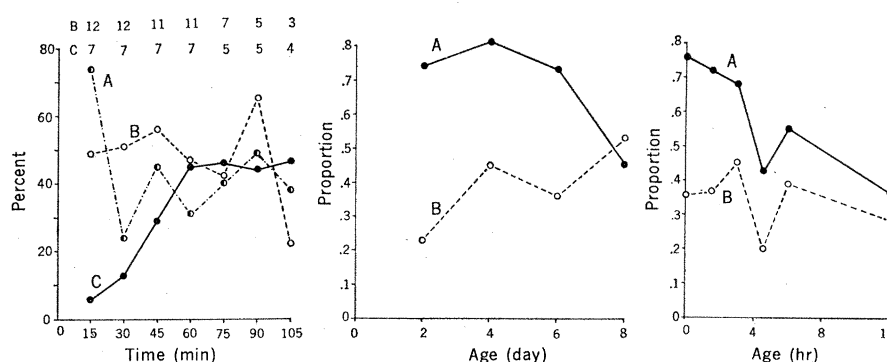


Fig. 1. (Left) Percentage of time spent by a female parasitoid in the half of the observation arena it had searched before, in successive 15-minute periods (experiment 1). A, Control in which one female was placed in a fresh tray; B, means for females that showed no discrimination; C, means for females that showed discrimination. Note that this discrimination was reduced with time as the fresh side was gradually contaminated with the odor. Numbers of replicates for B and C are shown above. (Middle) The proportion of parasitoid approaches which showed apparent odor recognition in treatment (A) and control (B), as a function of parasitoid age (experiment 2). Each point is the mean of four replicates, $P_{A=B} < .005$, $< .025$, $< .005$, and $< .750$, respectively. (Right) The proportion of parasitoid approaches which showed apparent odor recognition in treatment (A) and control (B), as a function of age of the odor (experiment 2). Each point is the mean of 12, 2, 3, 2, 2, and 4 replicates, $P_{A=B} < .005$, $< .050$, $< .050$, $< .050$, $< .500$, and $< .750$, respectively.

detect trail odors. In the first, the ability of *P. basizonus* females to detect their own odor was observed. The experimental arena provided a substrate similar to the forest floor, in which the parasitoids habitually search for hosts. The sand floor of a tray (60 by 60 by 5 cm) was covered with lichens, *Cladonia* spp. It was dimly illuminated from above with a central, shaded 100-watt lamp. The arena was ventilated through the tray walls. A barricade was placed across the middle of the arena at right angles to two sides. A female was liberated in one half of the tray, and the whole tray was covered with an acrylic plastic sheet. When the female had searched the litter for 5 to 6 hours, it was captured and the barricade was removed. The female was released again in the center of the tray and the amount of time it spent in each half of the arena was recorded. Observations on a female released in a fresh tray acted as a control. Study periods of up to 1¾ hours were necessary to establish a change in behavior.

A second experiment provided a more rapid assay for trail recognition. The arena was simpler and smaller. A tray (60 by 27 by 5 cm) was illuminated as before and lined with a sand base on which two plastic rings (15 cm in diameter and 5 cm in height) were placed 10 cm apart. The tray was covered as before. This closed the rings to form two cages within the tray. One cage was used as a control. A female parasitoid was introduced to the other cage and was allowed to search for 2 to 3 hours. The parasitoid and the two plastic rings were then removed. A sheet of thin plastic was placed over the arena top and the course of a newly introduced female was traced for 15 to 30 minutes onto the plastic in ink. These tracings showed the number of times a parasitoid entered the treatment or control area without changing its course (apparent nonrecognition). They also showed the times it approached but did not enter the control or treatment area and those entrances that occurred after clearly defined changes in the course of the parasitoid (apparent recognition). Only trails within 1.25 cm (the approximate length of a parasitoid) of the cage perimeter were used in the analysis (7). This method could not be used for testing self-recognition because females became hyperactive after being confined in the small cage.

In experiment 1, 19 female *P. basi-*

zonus of unknown age were tested. Seven individuals avoided the area that they had already searched and 12 did not (Fig. 1). The latter individuals may have been too old to recognize trail odors; in the second experiment, age proved to be an important factor. Experiment 2 established that females of the same species could recognize each other until after they were 6 days old (Fig. 1). Under natural conditions, females could probably recognize this odor throughout their life span. In the laboratory, where they were kept in small cages before the experiment, the substrate and atmosphere probably became saturated with the trail odor. Here acclimation to high concentrations could have raised the level of response to a threshold higher than the concentrations reached in the experiments. Females were able to detect the odor 4.5 hours after another female had been present (Fig. 1).

One test was made on each of all possible combinations of four coexisting species of ichneumonid parasitoid that attack the same host. Conspecific, congeneric, and intergeneric recognition of trails was evident (Table 1).

The behavior of the parasitoids suggests that the odor acts as an irritant. The longer they remain in an enclosed space, the more they wipe their antennae and mouthparts with their forelegs, a mild form of the behavior seen in the presence of the irritant vapor of ethyl acetate. They tend to move more rapidly with time (6) and remain close to the perimeter of the tray.

These results provide an explanation for the interference between searching parasitoids observed in several sets of data analyzed by Hassel and Varley (8).

Since female parasitoids can recognize and avoid the presence of others, the maximum level of their abundance in a given habitat may be determined by the concentration of the trail odor, rather than by the density of hosts, in that area. Therefore, parasitoid numbers would reach their peak while the host population continued to rise, allowing the host to escape the large mortality caused by parasitoids. Although the efficiency of individual parasitoids may be increased, the mortality caused in the host population is decreased. However, as females are compelled to emigrate from an area with a high parasitoid density because of their avoidance behavior, new host populations can be colonized and the survival probability of the parasitoid species improved.

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Pre-Cretaceous Flowering Plants: Further Evidence from Utah

Abstract. *Palm roots discovered in place in the Jurassic Arapien Shale Formation are further evidence for pre-Cretaceous flowering plants.*

Petrified palm logs comprising two species of *Palmoxylon*, as reported (1) from the Middle Jurassic Arapien Shale Formation near Redmond, Utah, were excavated from undisturbed beds within this formation. These represent the first definite flowering plants known from strata of pre-Cretaceous age. Three criteria are necessary in order to substantiate the validity of a proposed pre-Cretaceous Anthophyta.

First, the collection site must be Jurassic or earlier in age. Second, it must be demonstrated that the fossil was collected in place. Third, the fossil must be unquestionably related to the Anthophyta (Magnoliophyta).

Jurassic invertebrate fossils have been collected near the localities of both palm roots (*Rhizopalmoxylon* and *Palmoxylon simperi*). These include forms previously described by Reeside