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EFFECTS OF GASTER EXTRACT TRAIL CONCENTRATION ON THE TRAIL FOLLOWING BEHAVIOUR OF THE ARGENTINE ANT, *IRIDOMYRMEX HUMILIS* (MAYR)

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Abstract—In the Argentine ant, optimum trail following to gaster extracts was displayed to 0.1 and 1.0 equivalents/50 cm of circular trail. Trail following to airborne components was demonstrated when ants exhibited normal trail following behaviour while walking 3 or 6 mm below a 0.1 ant equivalent trail. However, at 8 or 12 mm separation, following ceased, indicating that the height of the active space was *ca.* 6–8 mm. The average horizontal distance from the centre of the trail at which ants exhibited following behaviour increased with concentration to 3–4 mm beyond the applied trail boundaries, indicating both an ability to follow airborne chemicals, and possibly a non-tolerance of excessively high concentration. Activity of 0.1 ant equivalent trails on filter paper declined to about half the original level by four hours; after eight hours, responses were significantly different from, but almost as low as, solvent controls.

Key Word Index: Argentine ant, *Iridomyrmex humilis*, trail following, bioassay, airborne trail

INTRODUCTION

DETAILED quantitative behavioural characterization of pheromonally-mediated social insect interactions has often lagged far behind isolation and identification of the compounds involved. The development of techniques for the measurement of relevant responses to pheromones in social insects, where context and motivation play active roles in the mediation of communication is, indeed, challenging and must be tailored to each species according to its biology (PASTEELS, 1975).

The Argentine ant, *Iridomyrmex humilis* Mayr, like most other dolichoderine ants, possesses a specialized gland in the gaster now called Pavan's gland after PAVAN and RONCHETTI (1955), which was demonstrated to be the source of trail pheromone (WILSON and PAVAN, 1959). Chemical characterization of this ant species as well as of other dolichoderine ants has been extensive (CAVILL *et al.*, 1956; TRAVE and PAVAN, 1956; CAVILL and HINTERBERGER, 1960, 1962; BLUM *et al.*, 1963; CAVILL and HOUGHTON, 1974; WHEELER *et al.*, 1975; CAVILL *et al.*, 1976; WHEELER *et al.*, 1977; CAVILL *et al.*, 1979, 1980). Considering the extreme importance of this ant in crops such as citrus, however, where workers tend and protect honeydew-producing insects from natural predators and parasites and can mean the difference between success or failure of natural control (DEBACH *et al.*, 1951a,b), it is surprising that virtually no quantitative studies have been conducted on its behaviour. This study presents techniques for measuring trail following in the Argentine ant, and provides an information base with which subsequent chemical–behavioural studies can be compared. We have: (1) determined the dosages eliciting optimum trail following to gaster extracts; (2) measured the vertical and horizontal aspects of the active space of trails; and (3) determined the longevity of gaster extract trails in the laboratory. This is the first in a series of behavioural studies of the Argentine ant recruitment system and the trail following mechanisms which are involved.

MATERIALS AND METHODS

Laboratory colonies of ants collected locally were maintained on a 14:10 L:D cycle in open foraging boxes, each containing several nest boxes. Taxonomic identity of each colony used was confirmed by ROY SNELLING of the Los Angeles County Museum. Ants were confined to the foraging boxes by electric barriers (WAGNER *et al.*, 1964), and nest boxes were connected with one another and with enclosed food dishes by teflon tubing so that foraging ants could be manipulated more easily. A circular metal foraging arena (75 cm diameter) could also be connected with the colony box by teflon tubing.

Trail application and bioassay

Extracts of worker ant gasters were made by macerating gasters in carbon disulphide or methylene dichloride and serially diluting this stock solution with solvent to yield solutions ranging in concentration from 10^{-4} to 5 ant equivalents/0.5 ml. Ants used to make these extracts were collected from foraging areas of laboratory colonies not engaged in food retrieval. Ants so chosen should be of more uniform age and trail pheromone content, following the findings for *Myrmica rubra* (CAMMAERTS-TRICOT, 1974; CAMMAERTS-TRICOT and VERHAEGHE, 1974).

Trails 50 cm in circumference were made similar to

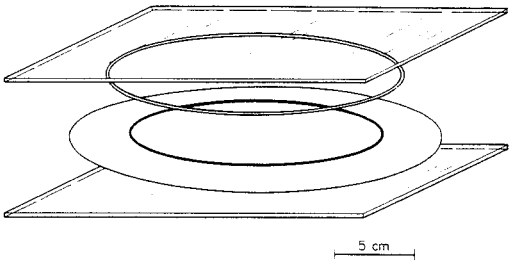

Fig. 2. Trail following assay arena, consisting of 2 glass plates, a spacer ring and the trail (heavy line) on a filter paper disc.

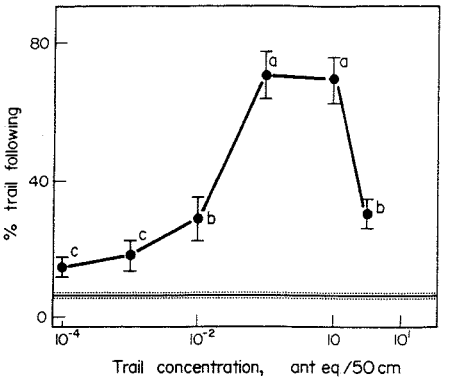

Fig. 3. Trail following response of ants to gaster extract trails ranging in concentration from 10^{-4} to 5.0 ant equivalents/50 cm, measured as the percentage of ants with 5 mm of the trail during observation periods. Standard error of responses to solvent controls is indicated by the shaded line. Brackets around means denote standard error. Means having no letters in common are significantly different according to Duncan's New Multiple Range Test ($P < 0.05$). $N = 20$.

TOPOFF *et al.* (1972), by siphoning 0.5 ml of extract from a calibrated reservoir through a teflon tube (size 30) onto a filter paper disc (Whatman No. 1, 24 cm diameter) rotating at 16 2/3 rpm. The tube tip contacted the paper disc making a continuous flow of extract for multiple revolutions (15–20) until the correct volume of extract was applied (Fig. 1). This technique was easy to use and provided trails which were uniform in concentration and had a solvent line approx. 2 mm wide, the solvent evaporating during each revolution before the next circular application of extract. The filter paper containing the trail was then housed under a glass plate suspended above the trail by a 3 mm spacer ring placed just inside the perimeter of the paper disc (Fig. 2). This chamber allowed ants to trail follow either in direct contact with the applied trail or upside-down on the glass plate suspended above it. Trail reinforcement was not observed during bioassay, and therefore responses during subsequent assays on a trail were due to experimentally applied trails.

Unless otherwise stated, ants were released individually in the centre of the chamber and observed for the next three min; during this period, the total time the ant spent within 5 mm of the trail and the number of times the ant entered this area (approaches) were recorded. By dividing the time spent in this area by the number of approaches, an index of trail following continuity (sec/approach) was calculated. All data were analyzed using Duncan's New Multiple Range Test.

Dose response

Initially, a dose–response curve was constructed by assaying groups of 10 ants to trails 10^{-4}, 10^{-3}, 10^{-2}, 10^{-1}, 10^{0} and 5 ant equivalents/50 cm trail in concentration. Ants were held briefly in groups of 10 in vials before being assayed. Upon introduction of all 10 ants to the centre of the circular trail as in RITTER *et al.* (1975), the number of ants within 5 mm of the trail was recorded each minute for 15 min. Two hundred ants were assayed at each concentration and each trail was used only once.

To determine whether distance from the trail at which ants exhibited trail following was dose-dependent, traces were made of the paths of ants following trails of various concentrations: 0.01, 0.1, 1.0 and 5.0 ant equivalents/50 cm trail. Traces were made during a 3 min assay of ants that had been isolated individually for 3 hr, and concurrently the total time spent trail following was recorded. To analyze these traces, the circular applied trail was divided into 10° arcs (Fig. 4). Only ant trace segments within each arc which did not describe an angle of more than 20° from parallel to the trail were scored. Thus, only tracings of trail following ants, not those of ants crossing the trail without following it, were measured in this way, the distance from the centre of each trace to the centre of the trail being the value recorded. The mean distance from the trail was calculated for multiple 10° arcs chosen at random from each of the 16 replicates/concentration.

Using information gained from the previous study, a new dose–response experiment was then conducted by assaying individual ants to trails 0.001, 0.01, 0.1, 1.0 and 5.0 ant equivalents in concentration. Ants from

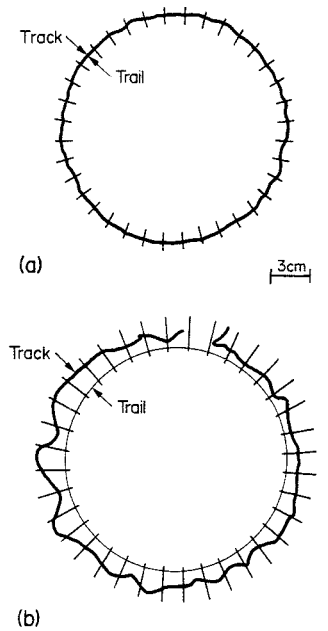

Fig. 4. Sample tracings of paths of trail following ants. (a) Trail concentration = 1.0 ant equivalent. (b) Trail concentration = 5.0 ant equivalents.

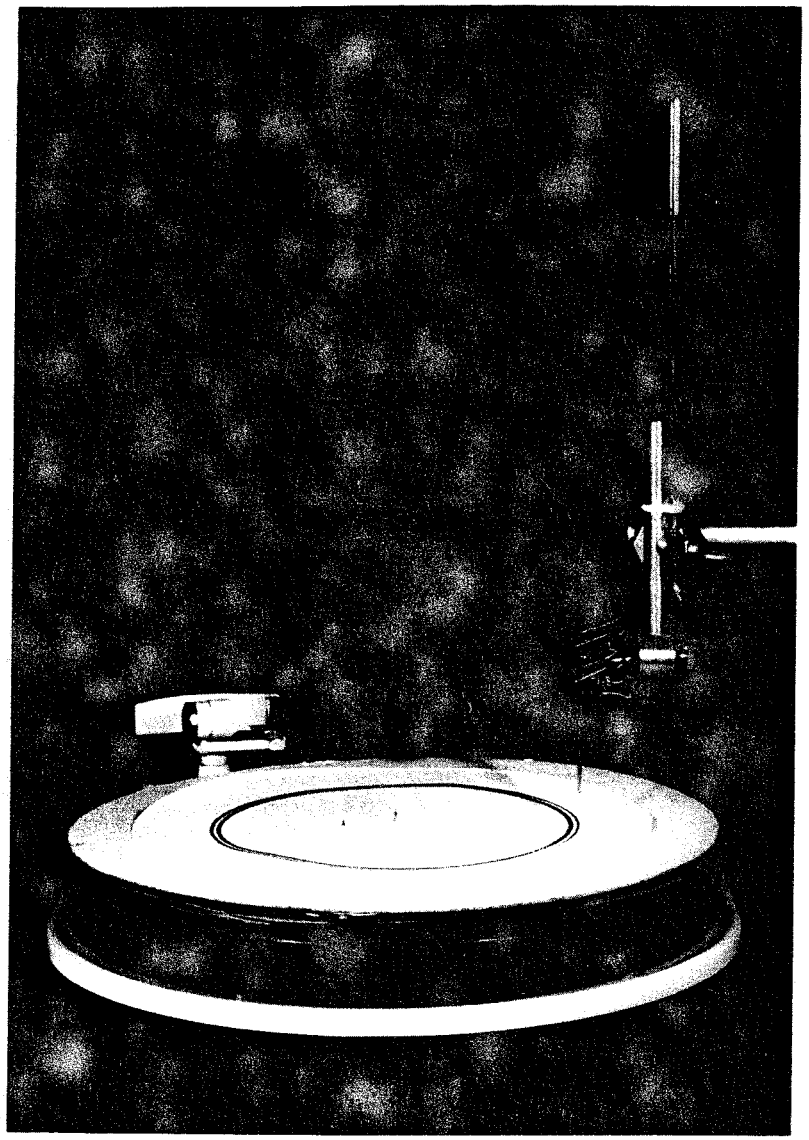

Fig. 1 Trail application apparatus including turntable, filter paper disc, calibrated reservoir and teflon tube.

the foraging arena were released in the centre of a trail-impregnated disc. Upon introduction to the assay chamber, each ant was observed for 3 min: during this time, the number of approaches to, and the time spent within 15 mm of, the trail were recorded. Twenty ants were assayed at each concentration and trails were replaced after 4 assays.

Airborne trail following

The dimensions of a trail's active space were determined by measuring the extent to which ants followed volatile trail components without contact with the applied trail. Ants were held in vials for 3–5 hr, then introduced individually to the centre of a glass plate above which a circular 0.1 ant equivalent trail on filter paper had been suspended. This concentration was the lower of the 2 dosages eliciting optimal trail following in dose–response experiments. The trail and the glass plate were separated by 3, 6, 8 or 12 mm by plastic spacer rings. By observing through the bottom of the glass plate, the total time during 5 min each ant spent within 5 mm of the lateral trail boundaries while on the glass plate was recorded. Twenty ants were assayed for each spacing, and 20 sec between assays were allowed for airing of the assay chamber. A mean duration of trail following for each distance of separation from the trail was then calculated.

Trail longevity

Longevity of trails applied on filter paper (0.1 ant equivalents/50 cm trail) was measured by monitoring trail following responses of recruited ants introduced directly onto the trail from a naturally-deposited trail. Again, ants were observed for 3 min, and the total time spent in the vicinity and the number of approaches to the trail were noted. Each trail was aged at room temperature (*ca* 23.5°C) in a fume hood (wind velocity = 0.15–0.3 m/sec) for 12, 8 or 4 hr. Newly-applied trails and solvent controls were also tested. The responses of 20 ants were measured on trails of each age. Trails were replaced after 5 assays, and assays were conducted in a randomized complete block design. Each trail was used for assay within 3.5 hr of its initial aging period.

RESULTS

Optimum trail following was found in response to trails of 0.1 and 1.0 ant equivalents/trail, but concentrations of 10^{-4} and 10^{-3} ant equivalents elicited low yet significant orientation to the trail (Fig. 3). Following was 50% lower at concentrations a decade below or above the optimum concentrations. No difference between blank controls and solvent controls was found.

Upon further examination, it was noticed that ants introduced to highly concentrated trails (5.0 ant equivalents) exhibited trail following-type behaviour (antennae down and moving side to side, walking parallel to the trail), but at much greater distances from the trail than allowed by the working distance initially chosen for bioassay scoring. By measuring the mean distance from the trail at which ants oriented parallel to the trail, an effect of trail concentration was demonstrated (Fig. 5). In response to trails of 5 ant equivalents, ants were found following almost 5 mm

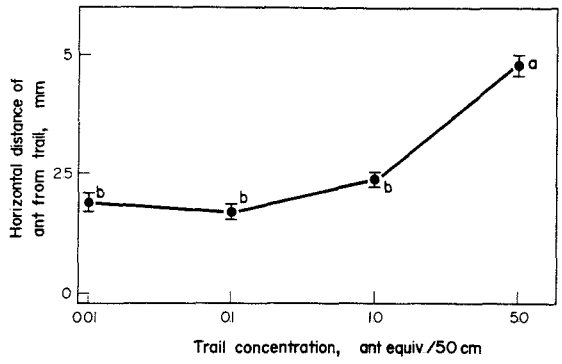

Fig. 5. Mean lateral distance (mm) from the applied trail at which ants exhibited trail following (see Fig. 4). $N = 159$–208 measurements (16 ants/concentration). Brackets around means denote standard error. Means having no letters in common are significantly different according to Duncan's New Multiple Range Test ($P < 0.05$).

on the average from the centre of the trail—well outside the solvent line and farther than ants orienting along less concentrated trails ($P < 0.05$).

Incorporating this fact into the bioassay by increasing from 5 to 15 mm the distance from the trail within which ants would be scored as trail following, we found that following does not decline at a concentration of 5.0 ant equivalents, but remains at the high level exhibited in response to the lower concentrations ($P < 0.05$), merely being displaced from the trail centre (Fig. 6).

Trail following decreased significantly in ants vertically separated from the trail by more than 6 cm (Fig. 7). Suspending the trail 3 mm above the glass plate did not prevent the ants from occasionally climbing from the plate back onto the filter paper above, but their response was recorded only when on the glass. While on the glass, ants trail followed with antennae brushing the substrate on which they were walking as if in direct contact with an applied trail.

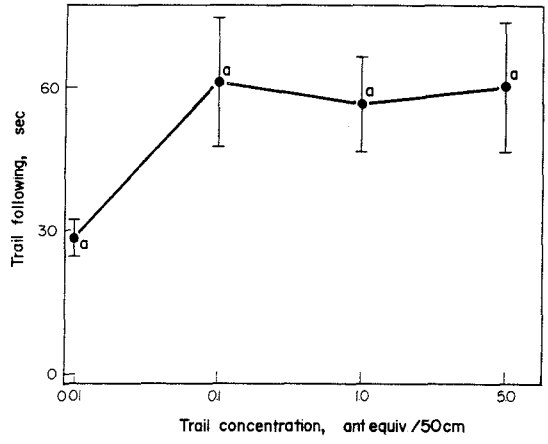

Fig. 6. Trail following response of ants to trails ranging in concentration from 10^{-4} to 5.0 ant equivalents/50 cm, measured as time spent (sec) within 15 mm of the applied trail during observation period. Brackets around means denote standard error. Means having no letters in common are significantly different according to Duncan's New Multiple Range Test ($P < 0.05$). $N = 16$.

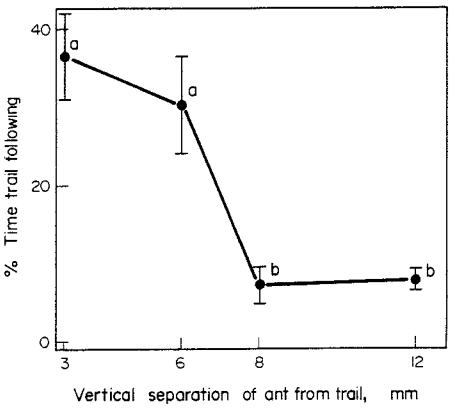

Fig. 7. Percentage of time ants spent trail following airborne components of 0.1 ant equivalent trails suspended 3, 6, 8 or 12 mm above them. Brackets around means denote standard error. Means having no letters in common are significantly different according to Duncan's New Multiple Range Test ($P < 0.05$). $N = 10$

even though in this case the trail was suspended above them.

Longevity of applied trails of gaster extract is shown in Fig. 8. Following continuity (sec following/no. approaches to trail) sharply declined to half its initial level by 4 hr and continued to rapidly disappear. No significant following was elicited by trails aged 8 hr or more ($P < 0.05$).

DISCUSSION

Trails are crucial to the survival of Argentine ant colonies. They are used for food retrieval during photophase and scotophase, and for the regular exchange of individuals. Workers seem to rely entirely on

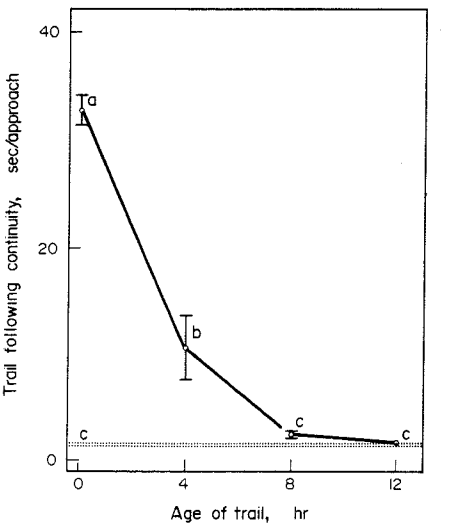

Fig. 8. Gaster extract longevity on filter paper under laboratory conditions, measured as trail following continuity (sec/approach). Trail concentration = 0.1 ant equivalents/50 cm. $N = 25$. Brackets around mean denote standard error. Means having no letters in common are significantly different according to Duncan's New Multiple Range Test ($P < 0.05$).

chemical cues for their orientation between nest a food sources, being possibly influenced topographic features of the environment, such edges, for the placement of chemical trails as sho for *Neivamyrmex nigrescens* (TOPOFF and LAWS 1979). To date there is no evidence for the use of vis cues such as landmarks or sun-compass orientatio this ant.

Argentine ants contain a multitude of vola chemicals, including many terpenoid compounds suc iridomyrmecin, which have insecticidal properties (CA and HOUGHTON, 1974). Volatile compounds wh have been characterized from gaster extracts incl 4-methylhexadecane, 3- and 5-monomethyl alka (C_{14}–C_{10}), (*Z*)-9-hexadecenal, 13-(1 methylpro tridecanolide and (*Z*)-10-nondecene-2-one (CAVIL *al.*, 1979). One of these compounds, (*Z* hexadecenal, is extremely active by itself in elici trail following behaviour (VAN VORHIS KEY BAKER, unpublished), and perhaps others may func as additional trail pheromone components. addition, it is possible that anal gland constitu mediate, as they do in other species, such behaviou activation, biting and dispersal. Gaster extr therefore contain many other potenti behaviourally-active compounds, and 'trail follow responses to these extracts could be complicate other reactions. This does not appear likely h however. First, there is apparently no al pheromone in this species with which to confo observations, and the responses observed were de of such behaviour as biting, etc. Further evidence responses reported here are, in fact, true responses to (a) trail pheromone component(s gaster extracts is that trail following is evoked by (*Z*)-9-hexadecenal (VAN VORHIS KEY and BA unpublished).

That trail-utilizing insects can orient to the vola of their trails has been noted previously (WIL 1971; RITTER and COENEN-SARABER, 1969). M and SILVERSTEIN (1967) found an effect of the dist above the trail at which *Atta texana* workers suspended on a plastic sheet filled with holes thr which volatile components of the trail below diffu TSCHINKEL and CLOSE (1973) suspended termite gauze above the trails to investigate reinforcement behaviour, and found incidentally the distance from the trail at which the gauze suspended did influence behaviour of the termites this effect was neither quantified nor explai Responses of *Atta sexdens* to a volatile pheromone component, methyl-4-methylpyrro carboxylate, were reported by ROBINSON and CHE (1975) who demonstrated its attractive qualitie unladen workers heading on trails toward foraging area from their nest. *Neivamyrmex nigres* workers could not only follow volatiles from t suspended 3 cm below them, but other vola emanating from ants laying trails beneath them ca increased trail following (TOPOFF and MIRE 1975). The 3 cm distance cannot be taken as a mea of the trail's vertical active distance, however, sinc arena was not designed for this purpose and may interfered with the even diffusion of the trail volat forcing the active space to assume a tall, narrow f

We used the ability of Argentine ant worker

follow the volatile components of trails of gaster extracts to obtain a measurement of the active space of trails of an optimal trail following concentration. The method described here was free of physical interruptions of the trail space and determined the trail's vertical 'active distance' to be 6–8 mm.

Assays designed for measuring trail following response in ants are often performed in the field to screen activities of possible trail pheromone components. Ants exiting their nest encounter an artificially applied trail, which they must follow for some arbitrary distance to be scored as responders. The context of introduction of the ant to the trail and the many factors contributing to the physiological and behavioural state of the ant are often overlooked or difficult to control. In addition, physical attributes of the trail such as its applied width, concentration, age and the substrate may be crucial to the response it elicits. The method of scoring for trail following in experimental situations can lead to ambiguous assessment of the 'activity' of test trails (RITTER and PERSOONS, 1976). Indeed, the differently shaped dose–response curves we obtained by changing the scoring criteria demonstrate the influence of dosage and sampling design on the results of trail following assays.

For the relatively small Argentine ant (*ca* 2.5 mm long, 0.5 mm wide), active trail columns can often reach several cm in width, but for a discriminating assay of these ants, a narrow trail is desirable. Also, they are easily disturbed by air currents and vibrations, and behaviour such as alarm may be released. Thus, a closed assay system utilizing highly uniform and consistent trails was essential, and the method for assessment of responses allowed for repeated exposure of the ant to the trail in the somewhat artificial bioassay conditions.

It remains to be seen which parameters measured, such as duration, continuity, distance travelled or some as yet undescribed behaviour will result in a more discriminating assay. More relevant, perhaps, are the speed of locomotion and measures such as angular deviation from the trail which may reflect the accuracy of orientation. Sinuosity of movement, speed of locomotion and attraction (angular orientation toward a source) have been measured for *Myrmica* workers responding to point sources of alarm pheromone components (CAMMAERTS-TRICOT, 1973; CAMMAERTS-TRICOT *et al.*, 1976; MORGAN *et al.*, 1977; and CAMMAERTS *et al.*, 1978).

That ants move outward and exhibit following in a zone away from highly concentrated trails may mean that a trail's 'active space' can be delimited by both lower and upper threshold concentrations. Upper thresholds were not included in BOSSERT and WILSON's (1963) models for active spaces of pheromone signals, and should certainly be considered in future calculations. There is evidence for the existence of such thresholds. In the Oriental fruit moth sex pheromone system, for example, an upper threshold was implicated in the premature termination of upwind flight by males to high emission rate sources causing the active space to be skewed away from the source (BAKER and ROELOFS, 1981). In our case, for the highest trail concentration, the active space also apparently was not contiguous with the deposited pheromone, being displaced laterally by a few mm. By turning, possibly tropotactic (HANGARTNER, 1967), at concentrations above an upper threshold or below a lower one, the ants would remain within an 'optimum' concentration. One alternative explanation is that once locating the lower threshold trail 'edge', the ants orient along it, never reaching the upper threshold concentration near the centre, since perhaps only one 'edge' or sharp gradient is necessary for trail following to be performed. Certainly, in the wide columns of Argentine ants found in nature, exaggerated zigzagging is not often observed, but would be expected if both 'edges' of the trail were necessary for accurate orientation. Detailed studies of such concentration effects may have practical significance in the design of control schemes. For example, ROBINSON and CHERRETI (1973) demonstrated that pickup of pheromone impregnated filter paper discs by three species of leafcutting ants decreased at high pheromone concentrations. Further experiments are being conducted to examine trail following mechanisms in Argentine ants.

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