

## AN INTEGUMENTARY PHEROMONE-SECRETING GLAND IN *ATTA* SP: TERRITORIAL MARKING WITH A COLONY- SPECIFIC PHEROMONE IN *ATTA CEPHALOTES*

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**Abstract**—Workers of *Atta cephalotes* mark the area around their nest with a pheromone that has at least two components, one of which is colony-specific. Another, which was isolated and tested for its activity, is genus- or species-specific in its action; it appears to be similar in *A. sexdens* and *A. cephalotes*, but differs in *Acromyrmex octospinosus*. The pheromone is produced in a newly described gland, located near the sting. A synthetic trail pheromone component in very low concentrations stimulates some behavioural effects similar to those of the territorial pheromone.

### INTRODUCTION

EARLY experiments of FIELDE (1904) on several species of American ant, mainly of the genera *Camponotus* and *Formica*, and later work by WALLIS (1962) on the wood ant, *Formica fusca*, showed that these insects recognize nest-mates and distinguish them from those of other colonies on the basis of odour signals. Foragers of the harvester ant, *Pogonomyrmex badius*, orientate to the nest odour when they are returning to the nest and are within close range and can be repelled by materials from the nests of other colonies of the same species (HANGARTNER *et al.*, 1970). BRIAN (1956) has suggested that the 'nest odour' may play a part in recognition of nest-mates in *Myrmica* species, and LANGE (1960) has made a similar suggestion for various species of *Formica*.

The existence of territorial behaviour has not been demonstrated clearly in ant colonies in the field. However, it is known that colonies of some species partition their activities in the environment. LESTON (1973) and MAJER (1972) found that an 'ant mosaic' exists on cocoa in West Africa. *Oecophylla longinoda* and *Macromischoides aculeatus* are both dominant species but are mutually exclusive; they fight or repel one another when they come into contact. Some species (e.g. *O. longinoda* and *Crematogaster castanea*) overlap in distribution and co-exist. HÖLLDOBLER (1976) found that the harvester ants *Pogonomyrmex barbatus* and *P. rugosus* partition the environment by establishing long-lasting chemical trails which do not overlap. When workers from two colonies of *P. barbatus* are induced to forage at the same food source, they fight fiercely when they come in contact and eventually develop divergent trails.

The use of pheromones to mark a general defended area has been recorded only in laboratory colonies of *Myrmica rubra* (CAMMAERTS *et al.*, 1977) and *Oecophylla longinoda* (HÖLLDOBLER and WILSON, 1977). In the former, the workers recruit nest-mates to

new territory with a recruitment pheromone from the Dufour's gland. Old territory is distinguished from a new one by means of a scent. *O. longinoda* workers mark their territory with spots of rectal sac secretions, and only defend successfully the territories marked with these spots by their nest-mates.

Colonies of attine ants partition their foraging areas in the field (see for example PEREIRA DA SILVA, 1975), and defence has been described in two species of *Atta*, which seems to be restricted to fighting when trails meet or cross (ROCKWOOD, 1973).

We have observed that laboratory colonies of *Atta cephalotes*, *Acromyrmex octospinosus* and *Atta sexdens* defend their general nest and foraging area against intruders of other colonies of the same or different species, but do not fight an alien when they are on unfamiliar territory. The following work demonstrates the existence of a territorial pheromone controlling this behaviour in *Atta cephalotes*.

### MATERIALS AND METHODS

#### *Insect cultures*

Four small colonies each of *Atta cephalotes* and *Acromyrmex octospinosus* (collected in Trinidad W.I.) and one of *Atta sexdens* reared from a swarming queen were cultured on pairs of tables (53 × 38 cm) in an insectary maintained at 28 ± 2°C and 70–90% r.h. with a 12 hr light:12 hr dark cycle. Nest chambers placed on one table, consisted initially of plastic boxes, and subsequently of inverted 1350 ml museum jars, on plaster of Paris bases. These were filled with fungus and brood as the size of the colony increased. Food (*Ligustrum vulgare*) was supplied on the second table, connected to the former by a wooden bridge. Only one experiment per day was performed on each colony, between 11.00 a.m. and 2.00 p.m. (lights out 4.00 p.m.).

### Gas-liquid chromatography (GLC)

A Pye-Unicam 104 chromatograph, fitted with a dual flame ionization detector was used in the chromatographic studies. All-glass columns of 2 mm internal diameter and 3 m length, were filled with 5% Carbowax 20 M on 100-120 mesh diatomite CLQ, AAW/DMCS treated, and conditioned at 220°C. The packing and supports were supplied by J. J. (Chromatography) Ltd., Kings Lynn (U.K.). The carrier gas was oxygen-free nitrogen (BOC, high purity) at a flow rate of 25 ml/min.

### Solid-sample gas chromatography

Ants were killed by plunging them into finely-crushed dry ice. The part to be examined was then snapped off, or the gland to be studied was dissected and inserted into a vial made from the lower part of a 230 mm Pasteur pipette and sealed at both ends. The sealed vial was placed in the solid-sample injector barrel, using the solid-sample injector of MORGAN and WADHAMS (1972), and heated at approx. 150°C for 5 min before it was crushed. The tissue sample and glass fragments were removed at the end of each GLC-run.

### Preparative gas chromatography

An all-glass splitter was used, as described in BAKER *et al.* (1976). The trapping system consisted of a removable, angled capillary line, manufactured from 1 mm internal diameter electrode tubes (Jencons Scientific Ltd., Herts, U.K.) and a solvent trap. A Pye-Unicam injector port-heater was used to maintain the splitter at least 15°C above the oven temperature. Samples were collected by passing the column eluent through 5 ml of diethyl ether (Koch Light Laboratories Ltd., U.K.) cooled in ice. A clean capillary line and trap was substituted for each fraction collected.

### Bioassays

Two different bioassays were used. Bioassay I served as a method for obtaining absolute values of the

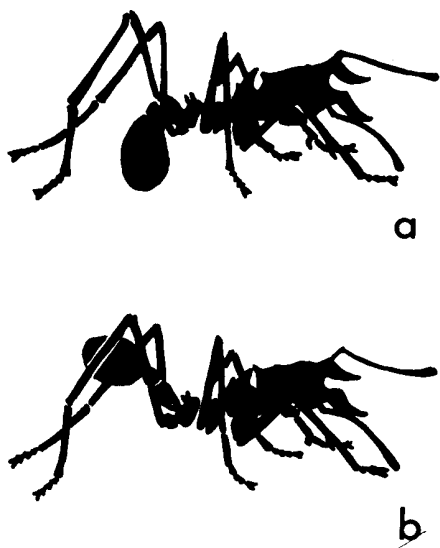


Fig. 1. *A. cephalotes* worker dipping the abdomen on the ground (a) and displaying abdomen raising behaviour (ARB), (b), on an unfamiliar territory.

response of the ants towards a sheet of paper which was used as an area of new territory. Bioassay II served as a rapid comparative measurement of the same response. In both bioassays, ants were allowed to forage on the nest table. Some ants followed a trail to the food source and others wandered over the total area of the table. Sheets of paper were placed on the table to one side of the food trail. The ants were initially alarmed when the paper was put in position, but some minutes later resumed their normal activity and many of them explored the new surface.

**Bioassay I.** A sheet of white duplicating paper (21 × 15 cm) was soaked with the solution to be tested or treated as otherwise specified in the text before being dried in air at 28°C for either 5 or 60 min (evaporation time). After drying, the paper was placed on the nest table. Thirty minutes later, after the ants had become familiar with the paper, those on the paper were observed. Some of the ants walking on the paper lifted their abdomens vertically (Fig. 1) and maintained this posture, which we call 'abdomen raising behaviour (ARB)', while on the new territory. The number of ants displaying either ARB or normal behaviour (NB) was counted during 5 min. The results were expressed as the percentage of ants showing ARB compared with the total number (ARB + NB) of ants observed on the paper during the 5 min period.

**Bioassay II.** One paper, identical to those described above, was soaked in the pure solvent, serving as a control, and another was soaked in the test solution or treated as otherwise specified in the text. Both papers were dried for 5 min in air at 28°C before they were placed simultaneously on the nest table. Ten minutes later, the ants were observed for a 3 min period. The positions of the papers were then reversed and the ants observed for a further 3 min period. In both observation periods, the number of ants displaying either ARB or NB were counted. The number of ants showing ARB was calculated as a percentage of the total number of ants observed (ARB + NB) for each sheet of paper. The value obtained for the experimental paper was divided by the value for the control, thus obtaining a ratio which quantifies the difference in ARB between both papers. Each final value is a mean of two ratios corresponding to the two alternative positions of the papers on the nest table.

## RESULTS

### Preliminary observations

If an *A. cephalotes* nest is connected to a new table with a wooden bridge, the ants advance slowly on to the new territory, dipping the tips of their abdomens on the ground or lifting their abdomens in the air (ARB) in a characteristic way (Fig. 1). Similar behaviour without abdomen dipping is observed if an ant is placed on the foraging table of a different colony. During abdomen-dipping behaviour the ants have their mandibles open, but not when trail-laying. Workers of *A. sexdens* and *Acromyrmex octospinosus* do not show ARB when exploring foreign territory, although they show dipping behaviour in the same situations as *A. cephalotes*.

Workers on a new table make only short individual

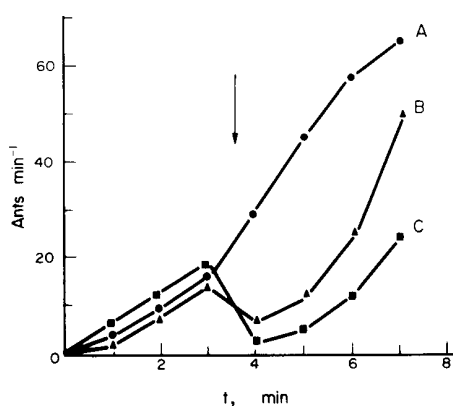


Fig. 2. Recruitment rate of workers arriving at a new table under normal conditions without external interference (A); with interference with food placed near the trail (B); with an artificial trail made with trail pheromone crossing the natural trail (C). ( $n = 5$ ). The arrow indicates the beginning of the interference in B and C.

explorations. Ants with no nest-mates in front of them turn back in the direction of the nest, eventually meeting nest-mates, in which case they normally begin their exploration again. The net result is as follows. The first ant walking on the new territory explores part of it, dipping the abdomen on the ground, and eventually turns back. Then a second ant will walk a little further than the previous one and so on: this continues until all the available area has been explored. When the area discovered is of a considerable size, the scouts recruit nest-mates with the help of a trail. This recruitment seems to be indistinguishable from the recruitment to a new food source (JAFFÉ and HOWSE, 1979). In both kinds of behaviour, the ants can be diverted from the trail by a food source placed close to the trail or by an artificial trail of methyl 4-methylpyrrole-2-carboxylate in ether (a synthetic component of the trail pheromone of *A. cephalotes*), laid across the existing trail (Fig. 2). An artificial trail made with the synthetic component of the trail pheromone, leading to a new table, will produce a recruitment pattern similar to that observed in normal and spontaneous recruitment to a new foraging table. With a naturally laid trail crossing new territory, 70.7% of all the ants that follow it leave before they reach the end. This percentage is almost identical ( $P > 0.95$ , Chi-squared test) to artificial trails crossing new territory (71.4%). That is, the response to both trails is the same. The artificial trail, leading to a new table, is reinforced by the ants after it has been used for about 5 min.

If a sheet of paper is placed on the nest table, the ants explore the paper surface and show both dipping behaviour and the ARB, but do not recruit nest-mates to the paper by the use of a trail.

#### Territorial marking

The possibility that ants mark their territories with a colony-specific pheromone was studied. Sheets of paper were placed on the nest table of colonies of: *A. cephalotes*, *Acromyrmex octospinosus* and *A. sexdens* for 48 hr. The papers were designated according to the species that had marked them as AC, AO, AS respectively. Bioassay I was used to measure the

Table 1. Comparison of the responses of *A. cephalotes* towards territories of different origins

Mean % of ARB:				
Control	AO	AS	AC	ACs
42.0	35.6	27.5	25.6	17.4
*****		*****		*****

Means joined by the same line are not significantly different ( $P < 0.05$ ). Continuous line: Hartley's test in Bioassay I; line of asterisks: Wilcoxon matched pairs test in Bioassay II (ANOVA,  $P < 0.001$ ). Each result is the mean of 8 replicates.

responses of *A. cephalotes* to the sheets of paper. If an AC paper was tested on the colony that marked it, it was designated ACs. A clean, untreated paper served as a control. The results (Table 1) show that the response to ACs and AC are different to those of AO and the control. Because the control paper cannot be marked in any way by the ants, this suggests that ACs and AC have been marked, probably by a pheromone, and therefore are recognized by the ants as such, and treated differently from the control. The marked territories of *A. sexdens* (AS sheets), produce the same response as the AC sheets. The territories of *Acromyrmex octospinosus* (AO) produce a significantly different response from those of AC. This suggests that the same, or a similar territorial marker pheromone is used by the two *Atta* species but not by the *Acromyrmex* species.

There is no significant difference between the papers from ACs and AC (Table 1) (Hartley's multiple range test), but if both papers are compared simultaneously using Bioassay II, with ACs as control and AC as the experimental group, there is a significant difference between them ( $P < 0.05$ , Wilcoxon matched pairs test). This suggests that ants mark their territory with a pheromone which has at least two components: a colony-specific one, recognized in ACs but absent or different in AC; and one which is species-specific (or genus-specific) present in AC and probably also in AS.

#### The gland used for territorial marking

(HÖLLDOBLER and WILSON (1977) showed that secretions of the rectal sac are used by the workers of *Oecophylla longinoda* to mark their territories. The nest tables of the three ant species studied here were covered with yellowish spots, produced by secretions from the rectal sac. For a study of the relationship between the number of rectal sac spots and ARB in *A. cephalotes*, sheets of paper were placed for 48 hr on different parts of the nest table of *A. cephalotes*

Table 2. Relationship between rectal sac secretion, measured as the number of yellow spots on a territory, and the amount of ARB as measured with Bioassay I

Type of territory; Spot density	Mean and standard deviation	
	No. of spots	% of ARB
Low (7)	2 ± 2	35 ± 10
High (8)	27 ± 6	29 ± 7
<i>t</i> -Test <i>P</i>	< 0.001	> 0.1

(7) And (8) are the number of replicates each using a different territory.

Table 3. Response of *A. cephalotes* towards different gland extracts, measured as the amount of ARB the extract induces in the ants using Bioassay I. (0.6 glands per paper)

Mean % of ARB:							
Sternal	Tergal	Dufour's	Meta-thoracic	Poison	Valves	AC	
53.6	53.3	47.1	46.7	43.9	29.6	23.3	

Means joined by the same line are not significantly different ( $P > 0.05$ , Hartley's test; ANOVA,  $P < 0.001$ ). Each result is the mean of 7 replicates.

colonies. The ants marked them to differing extents with rectal sac spots, depending on the distance of the paper from the nest. These papers were classified in accordance with the number of yellow spots and were placed on the nest table of other colonies of the same species. Bioassay I was used to measure ARB activity on these papers (Table 2). There is no significant relationship between the spot density and ARB when the effect of territories with high and low spot density is compared ( $P < 0.001$ , Chi-squared test).

In order to identify the gland used by *A. cephalotes* for territorial marking, ether extracts of different glands of workers of this species were applied to sheets of paper and were tested using Bioassay I. The glands used were: Dufour's gland, poison gland, metathoracic gland, sternal gland, tergal glands and the valves gland (BAZIRE-BENAZÉT and ZYLBERBERG, 1979). The concentration of the extract on the papers was approx. 0.6 gland equivalents per paper. The results (Table 3) show that the valves gland extract elicits ARB which is similar to that elicited by a naturally marked paper (AC) that had been placed for 48 hr on an *A. cephalotes* nest table. All other gland extracts tested show a significantly different response from that of AC. This suggests that the valves gland secretion is used by the ants to mark their territories.

If a paper of the type AC is left in still air for one hr at 27°C, a greater level of ARB occurs (as measured by Bioassay I) than with an AC paper left in similar conditions for 5 min (Table 4). The only gland extract that produces a similar effect is the valves gland extract. This confirms that this gland is the source of the territorial pheromone (at least of the species-specific component) in *A. cephalotes*. The relatively short-lasting effect of the valves gland extract suggests that the active component of the pheromone is a volatile substance. A period of 1 hr seems to be sufficient to allow the substance to volatilize to near or below threshold concentration.

The effect of the concentration of valves gland extracts on the ARB of *A. cephalotes* workers using Bioassay I is shown in Fig. 3.

Table 4. Effect of the evaporation time on the different gland extracts (0.6 glands per paper) on ARB measured with Bioassay I

Evaporation time in min	Mean % of ARB						
	Sternal	Tergal	Dufour's	Metathoracic	Poison	Valves	AC
5 (7)	53.6	53.3	47.1	46.7	43.9	29.6	23.3
60 (5)	48.7	50.2	45.6	46.8	29.8	41.3	37.8
<i>t</i> -test <i>P</i>	NS	NS	NS	NS	<0.01	<0.05	<0.05

(7) And (5) are the number of replicates for each mean %. NS = not significant ( $P > 0.05$ ).

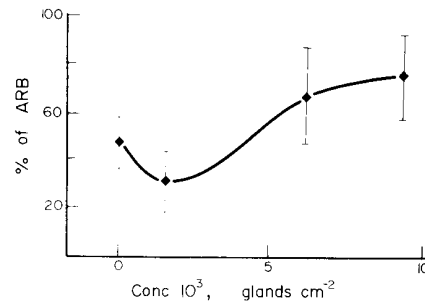


Fig. 3. ARB response of *A. cephalotes* towards different concentrations of the valves gland extracts, using Bioassay I.

The poison gland extracts elicit ARB if fresh, but after one hr of evaporation, they do not (Table 4). The synthetic trail pheromone component, methyl 4-methylpyrrole-2-carboxylate, is found to act in a similar way to the poison gland itself (Table 5). If the pyrrole is applied at a low concentration (Table 6) it does not elicit ARB, after 5 min evaporation time, but after 60 min the ARB response towards the extract is similar to that of controls. The pyrrole thus elicits ARB in concentrations in which it acts as a trail pheromone (JAFFÉ and HOWSE, 1979). In very low concentrations ( $\sim 0.2 \text{ pg. cm}^{-2}$ ), at which it no longer elicits trail-following responses, it has an effect on ARB similar to that of the territorial marker pheromone. If the trail pheromone is added to a previously marked paper (AC) and therefore presented simultaneously with the territorial pheromone, it does not then elicit ARB. Thus, the territorial pheromone can abolish the ARB response produced by the trail pheromone component. (Table 6).

#### Isolation of the marker pheromone

Gas-liquid chromatography was used to separate and isolate the different components of the valves gland and of the volatiles from whole gasters. Figure 4 shows the chromatograms of an *A. cephalotes* gaster. Component 64 is the only one that appears in the chromatograms of the valves glands in a quantity similar to the corresponding component in a chromatogram of the whole gaster.

Different fractions of the gaster, separated by gas-liquid chromatography, were collected (Fig. 4) in ether and tested for effects on *A. cephalotes*, using Bioassay II. Fraction 4 and fraction D elicit similar ARB in the ants to the valves gland extract (Table 7). This similarity is shown by the absolute value of ARB, by the concentration effect and by the behaviour occurring after 60 min of evaporation.

These results suggest that component 64 (Fig. 4)

Table 5. Effect of the synthetic trail pheromone on ARB of *A. cephalotes* measured with Bioassay I

Evaporation time in min	Mean % of ARB in experiments using	
	Poison gland (0.6 µl per paper)	Synthetic trail pheromone (2.5 ng per paper)
5 (7)	43.9	41.5
60 (5)	29.8	31.3
<i>t</i> -test <i>P</i>	<0.01	<0.05

(7) And (5) are the number of replicates for each mean.

Table 6. Effect of different concentrations of synthetic trail pheromone on ARB measured with Bioassay II

Evaporation time in min	% ARB experimental/% ARB control if trail pheromone is applied in the following concentration (ng per paper)			
	50	2.5	0.06	2.5 on AC paper
5	1.13*	1.03	0.65†	0.81*
60	0.83*	0.70*	1.12	—

\* =  $P < 0.05$ .

† =  $P < 0.01$ , Wilcoxon matched pairs test.

Each result is the mean of 8 replicates.

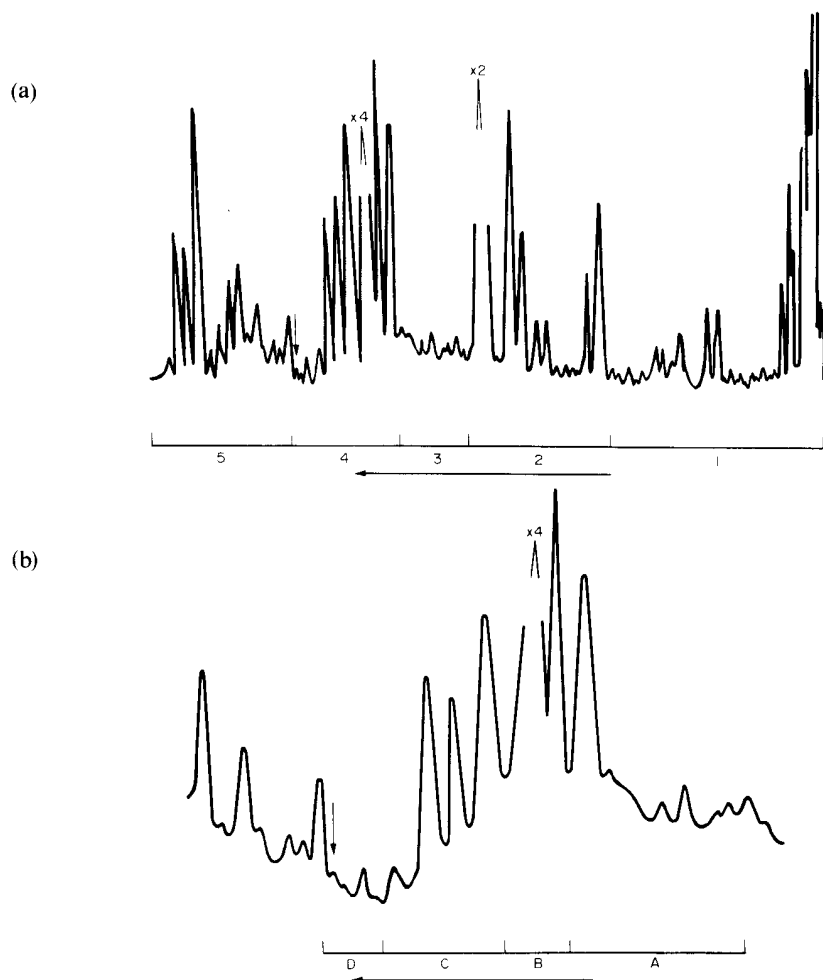


Fig. 4. (a) GLC-chromatogram of a gaster of an *A. cephalotes* worker. The component indicated with an arrow appears also in the valves gland chromatograms. The different fractions used in the bioassays are indicated below. (b) Amplification of the part of the chromatogram corresponding to fraction 4. Temperature programme: 70°C for 5 min, 2°C increase per min up to 210°C.

Table 7. Results from Bioassay II, comparing different GLC-fractions

GLC-fraction	Concentration in gland equivalents per paper		
	0.6	2.0	0.6 measured after 1 hr of evaporation
1	1.04	1.04	0.96
2	1.01	0.93	0.99
3	1.12*	0.94	0.97
4	0.79†	1.27*	1.03
5	1.00	1.45†	1.04
A	1.02	1.10	1.01
B	1.00	0.93	0.98
C	0.94	0.96	0.97
D	0.83†	1.27*	0.98
Valves gland extract	0.69†	1.51†	0.98
AC (Naturally marked)	0.69†	—	0.93

\* =  $P < 0.05$ .† =  $P < 0.01$ , Wilcoxon matched pairs test.

Each result is the mean of 7 replicates.

contains at least one species-specific component of the marker pheromone, indistinguishable in its effect from the secretion on naturally marked territories of the ants. This same component is also present in the chromatograms of whole gasters and valves glands of *A. sexdens*, but is not detected in *Acromyrmex octospinosus* gaster chromatograms in spite of the presence of valves glands in this species.

## DISCUSSION

These experiments show the existence in *A. cephalotes* of a territorial pheromone consisting of at least two different components. One is colony-specific and the other species-, or genus-specific. The species-specific component is produced by the valves gland (BAZIRE-BENAZÉT and ZYLBERBERG, 1979) and its effects last for approximately 1 hr.

The fact that the territorial pheromone here described is a rapidly-volatilizing substance, as in *Myrmica rubra* (CAMMAERTS *et al.*, 1977), suggests that territory marking in an ant colony is a continuous process, and is related to the degree to which the territory is exploited. An area which has not been marked by the colony for more than an hour may no longer be defended as a territory. The territory of an ant colony could thus be a constantly changing area without sharply defined borders. Its shape would depend on the location of the nest, the foraging sites exploited and the general activity level of the colony. These facts would be in agreement with observations made in the field by a number of authors (see for example PEREIRA DA SILVA, 1975; ROCKWOOD, 1973; CHERRETT, personal communication). Leaf-cutting ants in the field change their foraging sites frequently. They sometimes defend their trails aggressively against intruders, but peaceful interactions between ants from different colonies and species have been observed where foraging trails meet.

HÖLDOBLER (1976) suggested that the territory of an ant colony includes the areas immediately surrounding the nest and the foraging trails of the

colony. The similarity between the effects of the territorial pheromone and the trail pheromone in very low concentrations (250 times lower than in a normal recruitment trail), suggests that the trail pheromone is used as a marker of trunk trails. Thus, trails which are used constantly by the foragers for long periods of time do not need to be reinforced with fresh trail pheromone in the same way as a new recruitment trail. This mechanism would permit the ants to conserve trail pheromone, which they then could use extensively for recruitment trails, starting from the trunk trail. The trunk trails, although marked in a different way from the area surrounding the nest, can be then defended in a similar way.

Further behavioural studies on colonies of leaf-cutting ants in the field are required to determine the nature and significance of 'territory'. It appears from our experiments that territory in the conventional sense of a defended area exists in the immediate vicinity of the nest, and possibly in the areas where the ants are cutting their food. The trails are also defended, but are best regarded as separate entities.

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