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Communication in the migratory termite-hunting ant *Pachycondyla (= Termitopone) marginata* (Formicidae, Ponerinae)

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Abstract The Neotropical species *Pachycondyla marginata* conducts well-organized predatory raids on the termite species *Neocapritermes opacus* and frequently emigrates to new nest sites. During both activities the ants employ chemical trail communication. The trail pheromone orginates from the pygidial gland. Among the substances identified in the pygidial gland secretions, only citronellal was effective as a trail pheromone. Isopulegol elicited an increase in locomotory activity in the ants and may function as a synergist recruitment signal. The chemical signal is enhanced by a shaking display performed by the recruiting ant.

Key words Recruitment trails · Pheromones · Pygidial gland · Citronellal

Introduction

Several species in the ant subfamily Ponerinae are obligate termite predators (Hölldobler and Wilson 1990). This specialized feeding habit (termitophagy) occurs in three neotropical species in the ponerine genus *Pachycondyla (= Termitopone)*: *P. laevigata*, *P. commutata* and *P. marginata*. All three species exhibit group-raiding behavior aimed at termite nests, and they also relocate their nest sites in irregular intervals (Wheeler 1936; Hölldobler and Traniello 1980; Mill 1982, 1984).

The South American species *Pachycondyla marginata* (Roger) is widely distributed throughout Brazil (Kempf 1972). In the present study we report on a detailed behavioral analysis of its communication system including the chemical identification of the major trail pheromone components employed during foraging and nest emigration. Our experimental study in the laboratory is further complemented by field observations on the group-predatory and migratory habits of *P. marginata*. A detailed account on the ecology and field biology of this species is provided by Leal and Oliveira (unpubl.).

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Material and methods

Two colonies of *P. marginata* were collected in May 1993 in a semideciduous forest at the Santa Genebra Biological Reserve, Campinas, Southeast Brazil. The colonies were censused immediately after the careful excavation of the nests in the field. Colony I contained two queens, 602 workers and appr. 70 larvae. Colony II was queenless, and contained 1581 workers and ca. 280 larvae and 30 pupae. Major fractions of colonies III (ca. 500 workers) and IV (ca. 300 workers) were collected in September 1994. All four colonies were transported to the laboratory at the University of Würzburg (Germany), where the behavioral analysis was carried out. The colonies were housed in plexiglass arenas (35 cm × 85 cm) with a layer of gypsum covering the bottom. A depression (15 cm × 25 cm), subdivided into several champers, was carved out at one end of the arena and then covered with a red glass plate to provide a dark, moist nest cavity (see Hölldobler and Wilson 1994, p. 216). The ants had direct access to the arena, and for special experiments the nest arena was connected by paper bridges with one or two additional arenas, each measuring 70 × 140 cm.

Unfortunately *P. marginata* is highly specialized in its diet. We could maintain them, however, for appr. 6 weeks by providing cricket (*Acheta domesticus*) and cockroach nymphs (*Nauphoeta cinerea*) and a weak recruitment response could be elicited by offering to starved colonies nymphs of the termite species *Zootermopsis nevadensis*.

For histological investigations of exocrine glands we employed the methods described in Hölldobler et al. (1992).

For the behavioral tests of glandular secretions we dissected under water the following body parts out of *P. marginata* workers, which were killed by placing them for few minutes into a freezer: Dufour's gland, poison gland, hindgut, and pygidial gland. In a series of pilot tests the freshly dissected organs of single workers were smeared with the tips of hardwood applicator sticks over a sheet of paper placed onto the arena floor to create artificial trails of 20 cm in length. During the experiment a test trail and a control trail drawn with water or with one of the other glands were offered simultaneously, both starting at the same spot at the next entrance, but then deviating, so that they were approximately 10 cm apart at the end of the trail. The sides of the trails were regularly alternated, and for each tests a new paper was used. The number of ants that left the nest entrance and followed the trail during one minute intervals were recorded.

The chemical analyses of glandular secretions were carried out in the following way: From freshly killed *Pachycondyla marginata* workers pygidial glands were dissected under water and sealed in glass capillary tubes and by that means injected into the gas chromatograph without the intervention of a solvent (Morgan and Wadhams 1972). GC-MS analysis was carried out on a fused silica capillary column (0.22 mm × 25 m) coated with SE 52 in a Hewlett Packard 5890 gas chromatograph coupled to a Finnigan MAT 90 mass spectrometer. The glass capillaries were heated in the injection port at 220 °C for 2 min before crushing. The oven was held at 60 °C for 4 min before being raised to 260 °C at a rate of 6 °C per min.

In order to detect biologically active compounds, twenty *P. marginata* pygidial glands were extracted for 24 h in hexane (p.a., Merck). The micropreparative gas chromatogram was performed on a United Packard 438A instrument fitted with a 2 m × 4 mm glass column packed with SE 52. The oven was programmed as described above. Gland extracts were injected and different fractions were trapped in U-tubes cooled in Dry Ice. The material trapped was washed out with hexane and directly used for bioassays.

Additional details of the methods used for the behavioral analyses of identified substances are given with the description of the individual experiments.

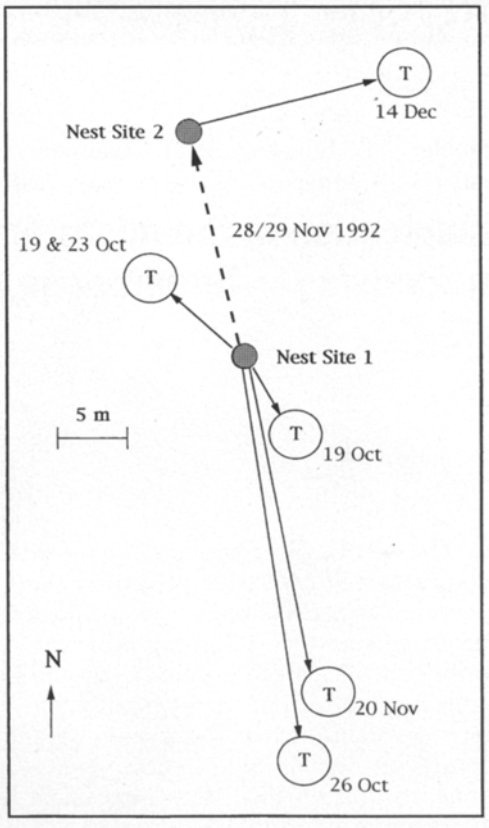

Fig. 1 Map showing one migration (*dashed arrow*) and five raiding routes (*solid arrows*) to termite nests (*T*) by a colony of *P. marginata* in a forest site in Southeast Brazil. The observations were made from 19 October to 14 December 1992

Results

Field observations

In the field *P. marginata* preyed exclusively on the termite species *Neocapritermes opacus* (Hagen) (Leal and Oliveira, in press). Target termite nests were 0.12-38 m far from the ant colony ($N = 202$, see Fig. 1). Raiding activity occurred day and night and could last for over 24 h.

The raiding process usually started with several ant workers leaving the nest in the same direction, possibly being already recruited by a scout ant. They all exhibited trail-laying behavior the pattern of which will be described in the next section. Upon finding a termite nest, the ants began to dig in preparation of an invasion of the nest. After nearly 20 min a few ants returned to their nest, also exhibiting the typical trail laying behavior. Shortly afterwards a column of *P. marginata* workers emerged from the nest and followed the trail toward the termite nest, walking slowly and frequently antennating nestmates they encountered on the way. Returning ants usually provoked the emergence of more and more nestmates from the colony of *P. marginata*, and this whole recruiting process could last up to 4 h before the first termite prey were retrieved by the ants. Raiding ants seized 1–2 paralysed prey specimens and returned to the nest. The speed with which the ants traveled along the raiding route increased with time, apparently due to the fact that over time more pheromone was deposited on the trail by raiding ants.

Like many other group raiding species, *P. marginata* also frequently emigrates to new nest sites. Migration of *P. marginata* colonies lasted 1–2 days and covered distances of 2–97 m ($N = 48$ Leal and Oliveira in press). A typical case history of such an emigration is based on one colony, which relocated its nest on 28. – 29. November 1992 (Fig. 1).

A group of 23 workers began to leave the nest at 16:15 h, exhibiting trail-laying behavior. The ants walked very slowly in a single column which was frequently interrupted. Twenty-five minutes later, after arriving at the new nest site (16 m away from the old nest), the ants excavated for approximately 2 h. During this period, 8 additional groups of ants arrived at the new site and also engaged in excavation activities. At 18:40 h the first larvae began to be transported from the old nest to the new one by a group of 31 workers. Eleven of these

workers were carrying larvae while the others exhibited trail-laying behavior. At this phase the ants moved much faster along the column, in a better organized fashion.

Pupae and eggs began to be transported to the new nest site at 19:10 h. Occasionally some workers were observed carrying termite prey from the old to the new nest. Both brood and termites were deposited in a small protected chamber near the main entrance of the new nest. Alates (males and virgin queens) began to leave the old nest at 20:00 h, being closely followed by many worker nestmates all the way to the new nest. Some alates entered the new nest, while others remained aggregated in the immediate vicinity of the main entrance. The migration to the new nest site continued throughout the night, and some workers were still observed walking towards the new nest at 7:00 h the next morning (a few were still carrying larvae). At 10:30 h the traffic of ants between the old and new nest sites had ceased and the whole relocation was apparently completed. All brood and termite prey were now housed in chambers deeper inside the nest. In all, the whole migration process lasted 18 h. We excavated the old nest and only found dead termites.

Since we had no *Neocapritermes opacus*, (the termite prey species), available in the laboratory, we focused on the communication mechanisms involved during nest emigration. We could, however, verify that the trail communication is identical during recruitment to termite nests and recruitment to new nest sites.

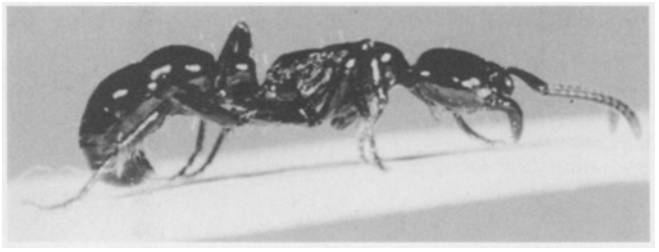

Fig. 2 Trail-laying *P. marginata* worker, bending the gaster forward and thereby exposing the applicator surface of the pygidial gland, which is touched to the ground

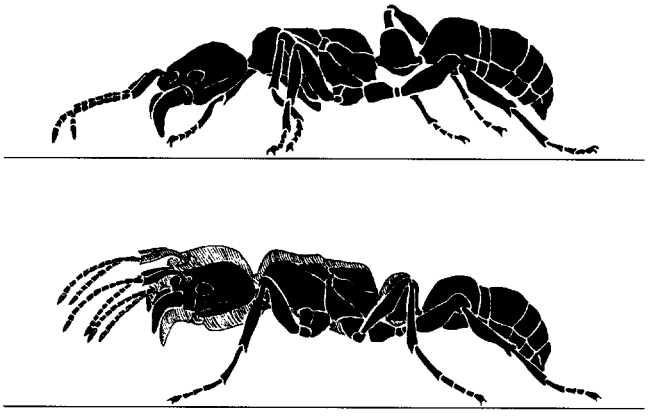

Fig. 3 Schematical drawing of the shaking behavior performed by a *P.marginata* worker inside the nest during the recruitment process. *Above*: worker walking into the nest. *Below*: worker performing the shaking display

Communication behavior during colony emigration

Emigrations could be elicited relatively easily by lifting the red glass plate that covered the nest chambers, and providing a new dark nest in an adjacent arena. The old and new arena were connected by a 40 cm long cardboard bridge. It could take between 22 min and more than 2 h before a scout had discovered the new nest. From that moment on the recruitment process commenced within approximately 30 min.

Scout ants began exploring the new area and finally returned to the old nest, obviously laying trails. The gaster was bent down and slightly forward, so that the last tergum was dragged over the surface (Fig. 2). During this procedure the gaster was slightly moved sideways from the right to the left side and then in the reversed direction at irregular intervals. This behavior closely resembles that described for trail laying *Pachycondyla laevigata* (Hölldobler and Traniello 1980). When the scout entered the old nest, some nestmates reacted by increasing their locomotory activity leaving the nest and some apparently followed the trail laid by the scout ant. These ants moved to the new nest, inspected it and also returned to the old nest exhibiting typical trail laying behavior. Finally one or several of those ants performed a striking motor display: a rapid, light, vertical shaking of the body, each bout lasting about a half second to 2 s (Fig. 3). Once nestmates encountered such shaking ants, some individuals reacted by shaking too, others started running towards the nest exit and soon many ants formed columns and moved along the trail of the scout ants toward the new nest site. A number of ants traveling in the column also exhibited trail laying behavior.

The trail laying posture strongly suggested that the trail pheromone in *P. marginata* originates from the pygidial gland, as it does in *P. laevigata* (Hölldobler and Traniello 1980). In fact, histological investigations showed that *P. marginata* has a very well-developed pygidial gland, consisting of paired clusters of glandular cells located dorsolaterally in the 6th abdominal segment. Each cell sends a duct through the intersegmental membrane between 6th and 7th terga. The gland is associated with an elaborate cuticular structure on the 7th tergum. The glandular secretions are apparently stored in the many cavities of this structure (Fig. 4). When laying trails the ant exposes this structure, which is normally covered by the 6th tergum, rubs the surface over the ground and thereby deposits the trail pheromone.

The behavioral tests of glandular secretions were very conclusive (Table 1). Only pygidial gland trails released trail following behavior in *P. marginata*. Hindgut contents and Durfour's gland secretions elicited

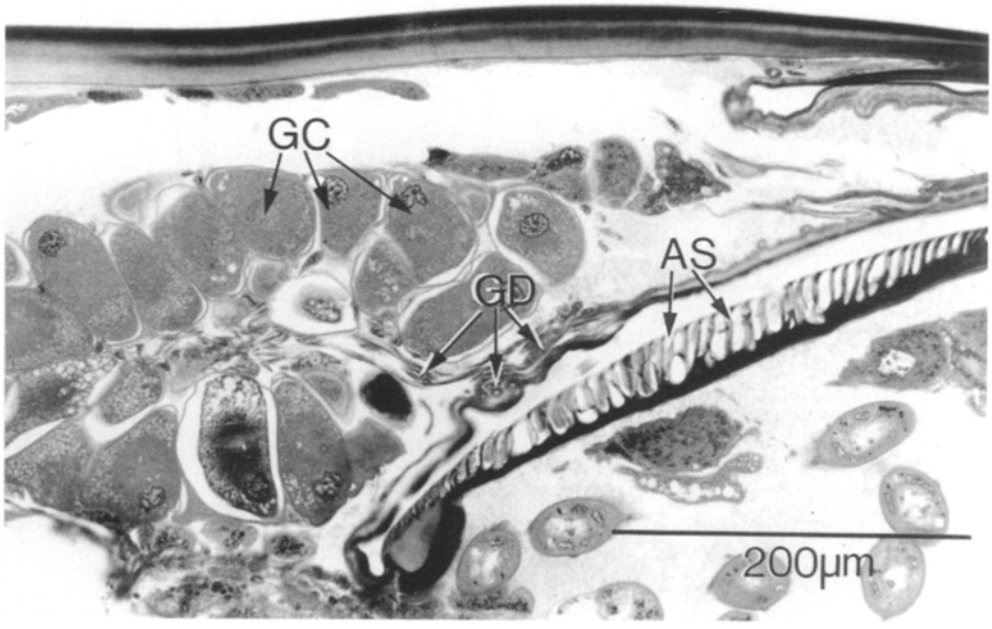

Fig. 4 Sagittal section through the pygidial gland, showing the cuticular structure of the applicator surface (*AS*), glandular cells (*GC*) and glandular ducts (*GD*) penetrating the intersegmental membrane

Table 1 Mean number of ants (± standard deviation, $N = 6$) leaving the nest (*A*) and following artificial trails drawn with the contents of one gland (*B*)

Pyridial gland		Hindgut		Poison gland		Dufour's gland	
A	B	A	B	A	B	A	B
32.7 ± 6.9	21.2 ± 6.6	3.7 ± 3.2	0	13.8 ± 2.9	0	4.3 ± 2.2	0

almost no noticeable response. When crushed poison glands were offered the number of ants leaving the nest increased and the ants displayed aggressive behavior. Most likely this secretion contains alarm pheromones. Also in this context the behavior of *P. marginata* resembles closely that of *P. laevigata*.

Pygidial gland contents alone not only releases trail following behavior, it also elicits a recruitment response, that is, the number of ants leaving the nest is much higher than that recorded when the other glandular secretions were presented at the nest entrance (see Table 1). The response was, however, even more pronounced, when the artificial trail was offered after a scout performed the shaking display inside the nest. We were able to conduct three experiments, where we allowed a group of scouts to enter the nest and then immediately covered the scouts' trails with paper sheets and subsequently offered artificial trails drawn with one pygidial gland each leading in a different direction than the scouts' trails. In all three experiments the number of ants leaving the nest was approximately 3 to 4 times higher, than when trails drawn with single pygidial glands were offered but no shaking display occurred inside the nest. It was impossible to take exact counts of ants leaving the nest, because the exodus was massive and sudden.

Chemical identification of the trail pheromone

In the gas chromatogram the pygidial secretion is dominated by 8 compounds (Fig. 5). Eluting later and not shown on this chromatogram are more abundant series of fatty acids and hydrocarbons. Peak *A* was identified as isopulegone, *B* as citronellal, *C* as isopulegol, *D* as citronellol and *H* as actinidine (Fig. 6). The structures that belong to the compounds *E*, *F* and *G* remain unknown; they have terpenoic characteristics in the mass spectra and GC-retention time.

From the micropreparative gas chromatogram and behavioral pilot tests we learned that only the fraction between 11 to 13 min elicited trail following behavior in *P. marginata* workers. This period included the four terpenes *A*, *B*, *C* and *D* which were subsequently tested in bioassays. For this purpose we obtained the four substances from commercial sources.

Citronellal which was later shown to be the effective trail pheromone, contains one chiral center and therefore two enantiomeres exist. The absolute configuration of the pygidial gland compound citronellal was analyzed on a capillary column coated with heptakis-(2,6-di-O-methyl-3-O-pentyl)-β-cyclodextrin (20% in Polysiloxane OV 1701). The oven was kept isothermally at 70 °C. Only one peak was detected for citronellal

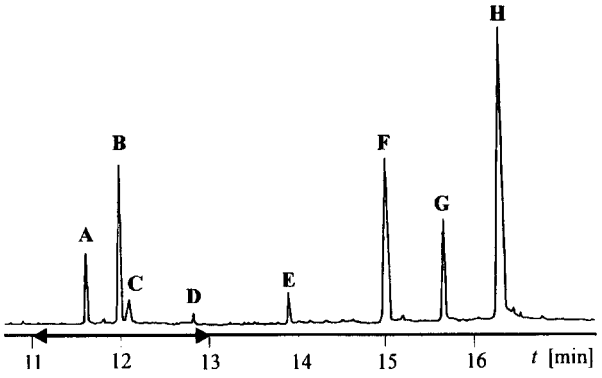

Fig. 5 Gas chromatogram obtained on a 25 m × 0.22 mm fused silica capillary column coated with a SE 52 stationary phase. The oven temperature was kept at 60 °C for 4 min and programmed at 6 °C/min to 260 °C. Ten pygidial glands of *P. marginata* workers were introduced by solid sample technique. *Thick arrow* marks the retention time of the biological active fraction. **A** isopulegone, **B** citronellal, **C** isopulegol, **D** citronellol, **E**, **F**, **G** unknown compounds, **H** actinidine

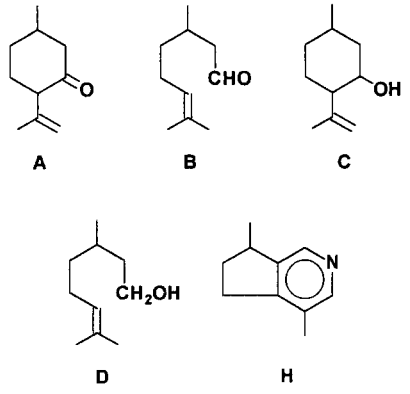

Fig. 6 Structures of the identified compounds in the pygidial gland secretions of *P. marginata*: **A** isopulegone; **B** citronellal; **C** isopulegol; **D** citronellol; **H** actinidine

in the *P. marginata* pygidial gland extract (Fig. 7). A comparison of the retention time of the gland volatile citronellal with the retention times obtained from a stereoisomeric mixture of (*R*/*S*) -citronellal (Fig. 7B) showed that the gland compound matched with the first-eluting (*S*)-isomer; i.e. more than 95% of the glandular citronellal represents the (*S*)-isomer (Fig. 7).

Bioassays of the identified substances

Following the methods described by Kern and Bestmann (1993) we took electroantennograms and obtained the best responses with citronellal and isopulegol, which were both significantly higher than that recorded with citronellol. The following trail tests, however, demonstrated that only citronellal elicits trail following behavior.

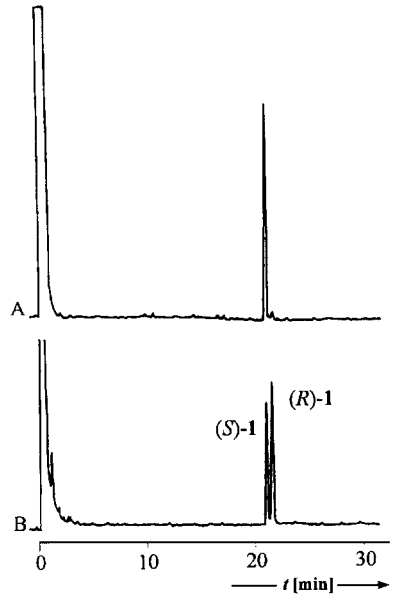

Fig. 7A, B Gas chromatogram obtained on a fused silica capillary column coated with heptakis-(2,6-di-O-methyl-3-O-pentyl)-β-cyclodextrin (20% in Polysiloxane OV 1701), isothermal at 70 °C. **A** Hexane extract 20 *P. marginata* pygidial glands, **B** Authentic sample of (*R*/*S*) -citronellal in a stereoisomeric mixture

One pygidial gland of a *P. marginata* worker contains approximately 20 ng citronellal. We offered artificial trails drawn on sheets of paper with different quantities of citronellal along a 20 cm long pencil line. The trails startet at the nest entrance of a *P. marginata* colony. When we applied ca. 10 pg – 100 pg of citronellal on the test trail no clear trail following could be observed, although some ants showed some trail orientation along a few centimeters of the pencil line. No such behavior was observed along a control trail drawn with 1 µl pure hexane. Clear trail following behavior (with ants moving along the entire trail) was, however, released when we applied 1 ng citronellal on the trail (1 µl of a solution of 1 µg citronellal in 1 ml solvent).

For the subsequent tests we used 10 ng of test substance on 20 cm long trails. Three trails were offered simultaneously, starting at the same spot at the nest entrance, but deviating, so that each trail was approximately 5 cm apart from the neighbor trail. One trail was drawn with citronellal, the other with citronellol and the third one with isopulegol. In subsequent tests the sides of the trails were alternated in a haphazard way. During 1 min periods all ants were counted which traveled to the end of each trail. At least 15 mins elapsed between each test. In one series of 7 tests, conducted with one *P. marginata* colony, 16.0 ± 8.9 ants followed along the citronellal trails, no ant followed the citronellol or the isopulegol trails. Similar results were obtained with a second colony, were 23.3 ± 10.6 ants followed the citronellal trails, none the other trails (see Fig. 8).

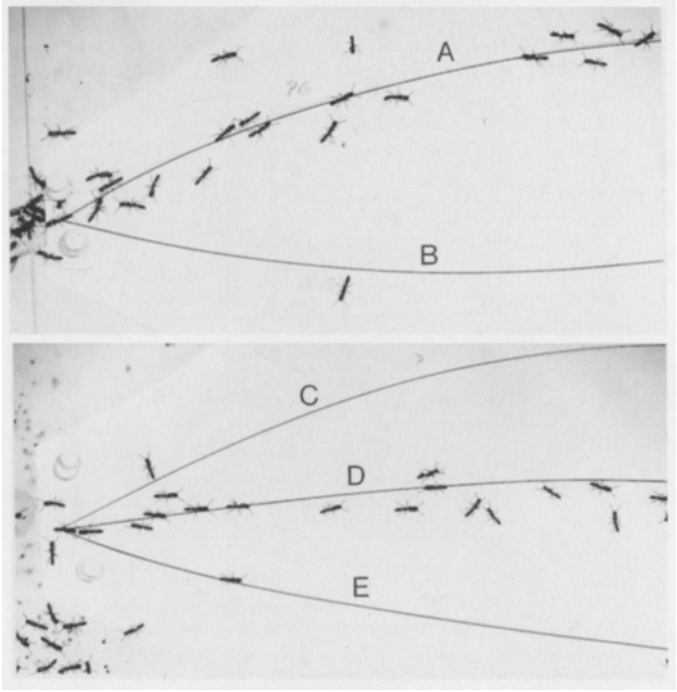

Fig. 8 *Above*: *P. marginata* workers were offered two trails, one drawn with pygidial gland contents (*A*), the other with hindgut contents (*B*). *Below*: *P. marginata* workers were offered simultaneously three artificially drawn trails; with isopulegol (*C*); with citronellal (*D*); with citronellol (*E*). As can be seen, the ants followed only the citronellal trail

We conducted 4 experiments during which we induced emigration columns along a 280 cm long trail drawn with 100 ng citronellal (100 µl from a solution of 1 µg citronellal in 1 ml solvent). In all tests a large number of ants followed the trails to the end although the ants had twice to cross a bridge connecting the two arenas.

Trails drawn with 10 ng citronellal along a 20 cm long pencil line still elicited orientation behavior in *P. marginata* workers, when offered 60 min after the trails were drawn.

Although the chemical analysis showed that the pygidial gland contained only the (*S*) -isomer of citronellal, in bioassays the ants responded equally well to trails drawn with the (*S*)- or (*R*) -isomer, respectively.

One pygidial gland of *P. marginata* workers contains only 3 ng citronellol and 1.5 ng isopulegol. Also with such small concentrations no trail following response could be released. However, when samples of 1–10 ng of isopulegol were presented inside the *Pachycondyla* nest, the ants responded by increased locomotory activity. Clusters of ants sitting almost motionless, started to dissolve when chips of filter paper carrying isopulegol were carefully placed in ca. 3 cm distance from the ants. No such reaction could be released with equal quantities of citronellol. We suspect, therefore, that isopulegol might function as an additional recruitment stimulus, once ants discharge pygidial gland secretions inside the nest.

Discussion

Pachycondyla marginata conducts well-organized predatory raids on the termite species *Neocapritermes opacus* and frequently emigrates to new nest sites (see also Leal and Oliveira, unpubl.). In the present paper we investigated the communication mechanisms involved in these social activities. Like in the closely related species *P. laevigata* (see Hölldobler and Traniello 1980) also in *P. marginata* the trail and recruitment pheromone originates from the pygidial gland. Neither hindgut material nor secretions from the Dufour's gland and poison gland elicit trail following behavior. Poison gland substance appears to release alarm behavior.

When nest emigrations are organized recruiting ants perform inside the nest a striking motor display that consists of rapid vertical shaking movements. Experiments indicate that this behavior enhances the effectiveness of pygidial gland secretions. The movement is very similar to that described for the ponerine ant *Prionopelta* where it serves as an alerting signal in the recruitment process (Hölldobler et al. 1992). In fact, the combination of mechanical and chemical signals in ant communication appears to be quite common (see Hölldobler 1995). For example in the ponerine ant *Odontomachus bauri* stimulating antennation bouts and chemical signals from the pygidial gland are implicated in the rudimentary recruitment communication (Oliveira and Hölldobler 1989).

The chemical analysis revealed (*S*) -citronellal as the major compound of the pygidial gland contents, and a series of bioassays demonstrated that this substance is the recruitment-trail pheromone of *P. marginata*. None of the other identified substances, such as citronellol and isopulegol releases trail following behavior. On citronellal, i.e. 1/10 gland equivalent, drawn out on a 20 cm long trail, was enough to elicit clear trail following behavior.

In plants citronellal (**B**) often occurs in addition with isopulegol (**C**) (William and Erman 1985). The aldehyde **B** is easily formed into **C** in a reversible reaction. Both terpenes are often accompanied by their reduction and oxidation products citronellol (**D**) and isopulegone (**A**). As only citronellal elicits trail following behavior in *P. marginata*, we suspect that the other terpenes, which occur in much lower quantities in the glandular secretions, may represent merely byproducts of citronellal. On the other hand, isopulegol produces better EAG-responses than the other "byproducts" and when offered inside the nest it appears to elicit an increase in locomotory activity. We are currently unable to decide whether this is an artifact caused by the similarity of isopulegol to citronellal or whether isopulegol represents a true synergistic releaser.

Citronellal has been found previously in the mandibular glands of several formicine ant species (see

Hölldobler and Wilson 1990) where it appears to function as an alarm pheromone. It had hitherto not been detected in ponerine species and our investigations provide the first record that this substance functions as a recruitment-trail pheromone in ants. We also identified actinidine in the pygidial gland secretions, but could not determine any behavior modifying function of this substance in *P. marginata*. Actinidine also occurs in the pygidial gland secretions of the termite hunting ponerine species *Megaponera foetens*, where it elicits alarm reactions (Janssen et al. in press), and in several dolichoderine species it may function as a repellent substance (Wheeler et al. 1977; Tomalski et al. 1987).

Investigations during the last 15 years demonstrated that the pygidial gland is an important pheromone gland in ants, and especially in ponerine species it often produces recruitment pheromones (see Hölldobler and Wilson 1990). For example in the genus *Leptogenys* the pygidial gland secretions serve as a recruitment trail pheromone in conjunction with poison gland substance (Maschwitz and Schönegge 1977; Maschwitz and Steghaus-Kovac 1991). The recruitment pheromone from the pygidial gland is cis-isogeraniol (Attygalle et al. 1991) and the effective orientation signal contained in the poison gland secretion is 4-methyl-3-heptanol (Attygalle et al. 1988). A similar situation we recently discovered in *Megaponera foetens* (Hölldobler et al. 1994). The pygidial gland pheromone, the chemistry of which is not yet entirely known, is a short lasting recruitment signal and the effective longer lasting trail pheromone from the poison gland is dimethyl uracil (Janssen et al. in press). Also in army ants the pygidial gland is involved in recruitment and trail laying. Hölldobler and Traniello (1980) pointed out that in *Neivamyrmex* and *Eciton*, secretions from the pygidial- and postpygidial gland elicit trail following behavior. Recently Oldham et al. (1994) identified in the army ant genus *Aenictus* methyl anthranilate and methyl nicotinate in the postpygidial gland and demonstrated that both substances play different roles in the recruitment and trail following process.

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