Ethology 83, 154—166 (1989)

ISSN 0179-1613

Department of Organismic and Evolutionary Biology,
Museum of Comparative Zoology Laboratories, Harvard University, Cambridge

Orientation and Communication in the Neotropical Ant *Odontomachus bauri* Emery (Hymenoptera, Formicidae, Ponerinae)

PAULO S. OLIVEIRA & BERT HÖLLDOBLER

OLIVEIRA, P. S. & HÖLLDOBLER, B. 1989: Orientation and communication in the Neotropical ant *Odontomachus bauri* Emery (Hymenoptera, Formicidae, Ponerinae). Ethology 83, 154—166.

Abstract

The Neotropical species *Odontomachus bauri* employs canopy orientation during foraging and homing. An artificial canopy pattern above the ants is much more effective as an orientation cue than horizontal landmarks or chemical marks. However, both horizontal visual cues and chemical marks on the ground can serve in localizing the nest entrance. Successful *O. bauri* foragers recruit nestmates to leave the nest and search for food. However, the recruitment signals do not contain directional information. Antennation bouts and pheromones from the pygidial gland most likely serve as stimulating recruitment signals. Secretions from the mandibular and poison gland elicit alarm and attack behavior.

Corresponding author: Bert HÖLLDOBLER, Zoologisches Institut, Universität Würzburg, Röntgenring 10, D-8700 Würzburg.

Introduction

The ant genus *Odontomachus* is pantropical in distribution and includes more than a hundred species which live in a variety of different habitats, ranging from rainforest to semi-arid environments (BROWN 1976). The nests are usually located in the ground or under rotten logs, rocks and fallen bark; some species are known to have arboreal nests (BROWN 1976). Colonies of *Odontomachus* can contain up to a few hundred workers which forage individually for living prey on the ground, or on trunks and foliage of trees. These ants possess highly specialized snapping mandibles which are very efficient for capturing prey, particularly soft-bodied arthropods (FOWLER 1980; DEJEAN & BASHINGWA 1985; DEJEAN 1988; CARLIN & GLADSTEIN 1989). Although widely considered as

U.S. Copyright Clearance Center Code Statement: 0179-1613/89/8302-0154$02.50/0

typically predatory ants, some species are also known to feed on honeydew from Homoptera (Evans & Leston 1971) and secretions from extrafloral nectaries (Schemske 1982).

Very little is known about the communication system of *Odontomachus*. Wheeler & Blum (1973) identified alkylpyrazine as an alarm pheromone in the mandibular gland secretions of *Odontomachus hastatus*, *O. clarus* and *O. brunneus*, and Jaffe & Marcuse (1983) studied nestmate discrimination in *O. bauri*. There are conflicting statements concerning the ability of *Odontomachus* to recruit nestmates to food sources. Jaffe & Marcuse (1983) state that *O. bauri* does not recruit to live arthropod prey, while Carlin & Gladstein (1989) report recruitment to dilute honey in *O. ruginodis*, though no trail-laying behavior was observed and the behavioral mechanism involved in recruitment is unknown. Dejean et al. (1984) mention that workers of *O. troglodytes* mark the colony's territory by depositing "anal products", whereas Jaffe & Marcuse (1983) were unable to demonstrate territorial marking in *O. bauri*. However, in both studies it was pointed out that visual cues might play an important role in home range orientation.

We conducted a laboratory study to resolve some of the contradictions in the literature, and to analyze in greater detail the behavioral mechanisms involved in home range orientation in *Odontomachus*.

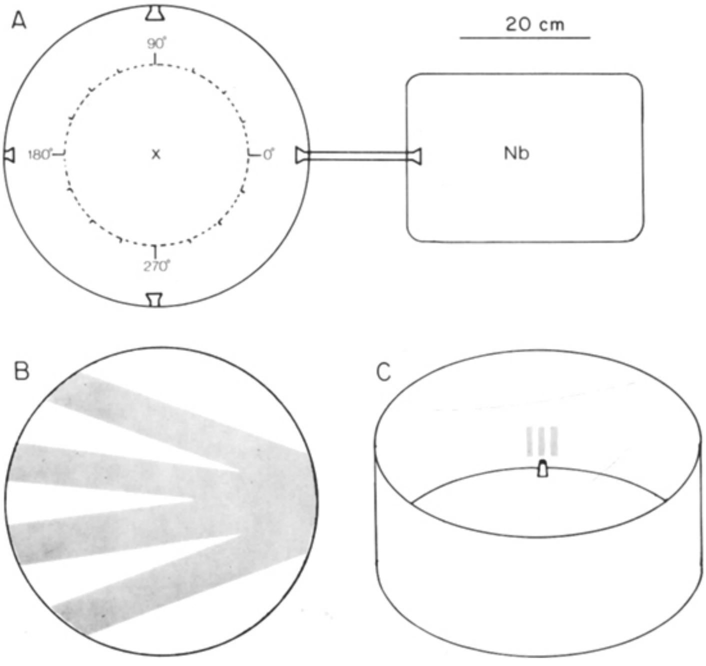

Fig. 1: Artificial setting for the orientation experiments with *Odontomachus bauri*. A) Nest box (Nb) and round foraging arena; the food source was always placed at the center (X) of the arena. B) Artificial canopy consisting of four cardboard stripes, which was placed on the top of the round arena at varying positions, depending on the experimental arrangement. C) View of the round arena showing the horizontal landmark directly above the nest bridge at 0°

Materials and Methods

The colony of *Odontomachus bauri* used in this study was collected in the rainforest of Barro Colorado Island (Panama) in Sep. 1987, in the leaf litter under a log (S. PRATT, pers. comm.). The ants were cultured at 20—25 °C, in the laboratories of the Museum of Comparative Zoology, Harvard University. By Nov. 1988, at the beginning of our observations, the colony consisted of one mated and one virgin queen, 165 workers, 31 pupae, 104 larvae and many eggs. The colony was housed in 8 glass test tubes (2.2 cm diameter × 15 cm) containing water trapped at the end behind a cotton plug. All test tubes were placed in a nest box (38 × 27 cm) which was connected to different foraging arenas, depending on the experimental arrangements. The ants were fed with live cockroaches, frozen *Drosophila*, dilute honey and synthetic ant diet (BHATKAR & WHITCOMB 1970). Glandular dissections were performed in distilled water on ants killed by placing them for a few min in a freezer.

The orientation experiments were performed in a round arena (51 cm diameter), which was completely surrounded by white walls (26 cm high) and diffusely illuminated from above by neon lights through a translucent plexiglass plate. A small cardboard bridge at 0° linked the arena to the entrance tube of the nest box. Thus the correct homing direction in the arena was toward 0°. Identical control bridges, which did not lead to exits, were placed around the circumference at 90°, 180° and 270° (Fig. 1A). The homing directions of the ants carrying prey were recorded as they crossed a circle (15 cm radius) drawn around a food source in the center of the arena. A mean vector of all homing directions of 40 individuals was calculated for each experimental series. The length of the vector ($0 < r < 1$) is a measure of the dispersion around the mean direction. These calculations and the statistical comparisons were based on BATSCHELET (1965). Further methodological details will be given with the description of the individual experiments.

Results

Home Range Orientation

From the beginning of our study we noticed that *Odontomachus bauri* foragers frequently raised their heads (3—5 times per min) when they entered a new terrain (Fig. 2). This behavior was rarely seen inside the nest tubes. A similar behavior was previously observed in the African ponerine ant *Paltothyreus tarsatus*, and HÖLLDOBLER (1980) subsequently demonstrated that this ant uses the pattern of the forest canopy as an important orientation cue. Since *O. bauri* inhabits forested areas in the Neotropics, we speculated that its head-raising behavior could also be related to canopy orientation. To test canopy orientation in *O. bauri* we conducted the experiments described below.

We placed on the top of the round foraging arena a glass plate onto which we had arranged four black cardboard stripes converging toward the nest entrance at 0° (Fig. 1B). The ants were allowed to habituate to this canopy pattern for one week, and during this time they were fed with dilute honey and frozen *Drosophila* at the center of the arena. The access of ants to the arena could be controlled by a sliding door at the entrance. When we finally conducted the tests, not more than two ants were allowed to search for *Drosophila* flies at the center of the arena. No individual ant was used more than three times during one session. Tested individuals were kept isolated as they entered the nest box with a prey item. In one set of experiments the arena contained a papered floor on which the ants had already foraged for 3—6 days. It is possible that this floor might have been marked with chemical cues which could affect the visual orientation. In another set of experiments we provided a fresh paper floor which was replaced after 20 ants had been tested. At this time we also replaced the nest bridge at 0° with a new one. The experimental manipulation consisted of rotating the canopy pattern in a given direction while individual ants were inspecting prey (15—20 flies) at the center of the arena (ants spent at least 15 s inspecting before retrieving prey). In control experiments ants with prey returned to the nest beneath an unaltered canopy. All experiments were carried out in intermittent sessions between 11.00 and 17.00 h.

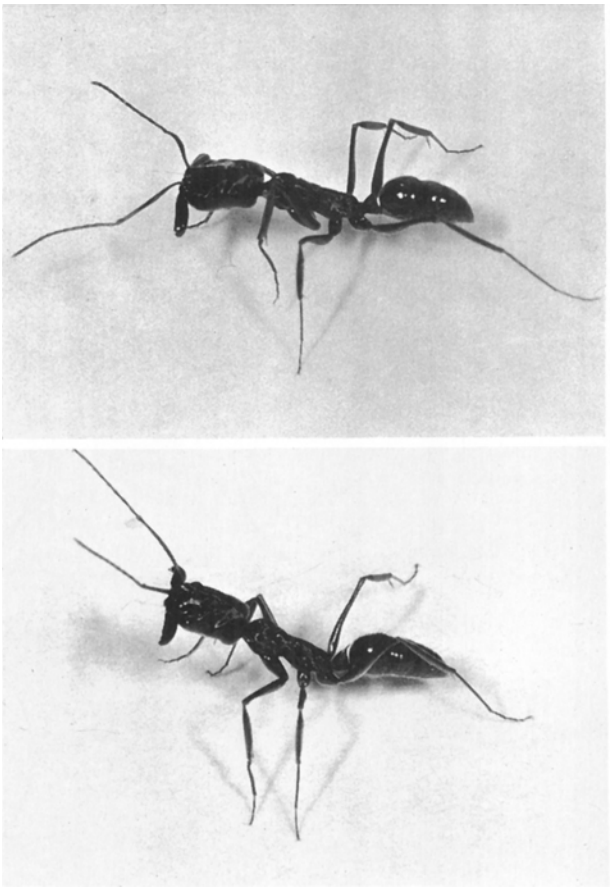

Fig. 2: Workers of *Odontomachus bauri* in normal posture (above) and in the typical head-raising behavior (below)

The results clearly demonstrated that the canopy pattern plays a major role in the homing orientation of *O. bauri* foragers. Irrespective of the condition of the papered floor, when the canopy is rotated for 90° or 270° the ants' mean homing direction is affected in accordance with the canopy rotation (Fig. 3A—C). The comparison between the experiments rotating the canopy for 90° and 270° also reveals that the ants discriminate between artificial canopies which have stripes converging in opposite directions. Surprisingly this ability was not expressed when we rotated the canopy for 180°. In this case the ants did not, as we would have expected, orient toward the opposite direction of the true homing route. Instead, their homing courses were either random (on a fresh paper floor), or pointed toward approximately 50° when tested on an used paper floor (Fig. 3D).

Although the canopy plays a major role in the homing orientation of *O. bauri*, the above experiments indicated that additional cues might be involved. This suggestion is supported by the following facts: The ants' homing orientation

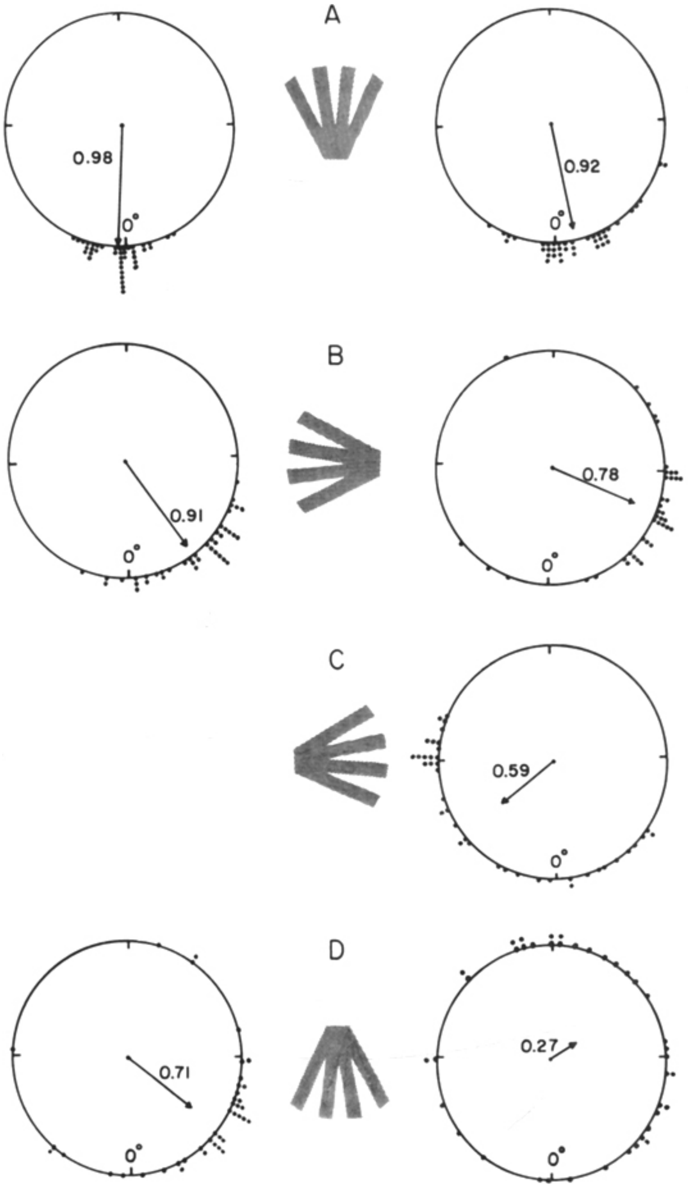

Fig. 3: Homing directions of foragers of *Odontomachus bauri* beneath different canopy patterns. The length of the mean vector ($0 < r < 1$) is a measure of the dispersion around the mean; unless otherwise mentioned, all vectors were statistically significant. Left: experiments on old papered floors, right: on new papered floors. A) Unaltered canopies at 0°; mean vectors differed significantly from each other ($F = 13.8$, $p < 0.001$, $df = 78$). B) Canopies rotated for 90°; mean vectors differed significantly from each other ($F = 15.1$, $p < 0.001$, $df = 78$). C) Canopy rotated for 270°. D) Canopies rotated for 180°; the mean direction on a new papered floor is not significant ($z = 2.9$, $p > 0.05$)

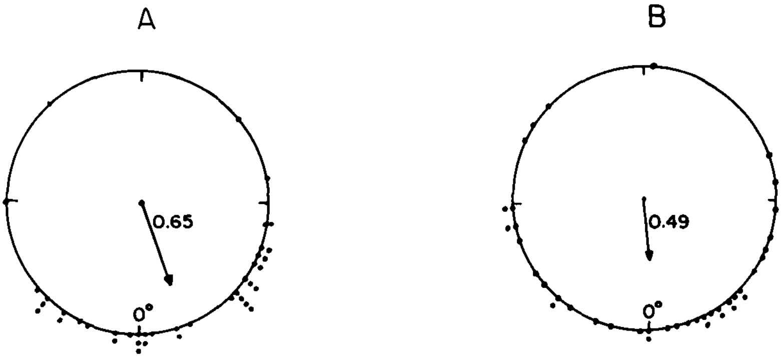

Fig. 4: Homing directions of foragers of *Odontomachus bauri* when no canopy is available. A) Old papered floor; B) new papered floor. Mean vectors are significant, and do not differ from each other (F = 1.04, p > 0.25, df = 78)

beneath a 90°-rotated canopy corresponded quite well with the one expected if the canopy pattern was to provide the major cue, but mean homing directions on old paper floors were always significantly different from those on new ones (Fig. 3A, B, D). These results suggest that chemical markers may serve as additional homing cues.

To test whether an old paper floor could contain orientation cues for the ants, we removed the canopy pattern while the ants were handling the prey at the center of the arena. We then compared the homing behavior of foragers on a 6 day-old paper floor with that on a new one. In both experiments the mean homing routes of the ants pointed approximately toward the nest entrance, and the mean vectors were not significantly different from each other (Fig. 4). We noticed, however, that the ants took longer to find the nest bridge on a new paper floor than on an old one (Table 1). Of course, we cannot rule out the possibility that foragers entering the arena might mark the floor with chemical homing cues. The only difference between old and new paper floors would then be the degree of marking. Although we do not have direct evidence, these results strongly suggest that chemical markers may provide at least residual orientation cues for homing *O. bauri* foragers, and may in fact be more important for localizing the nest entrance.

Table 1: Time to find nest bridge by ants homing on a fresh and an old paper floor (no canopy pattern available). Statistical comparison made through G-test of independence

Condition of paper floor	Ants finding nest bridge (in s)				p value
	≤ 15	16—30	31—45	≥ 46	
Fresh (n = 34 ants)	14	2	8	10	< 0.01
Old (n = 37 ants)	16	12	2	7	

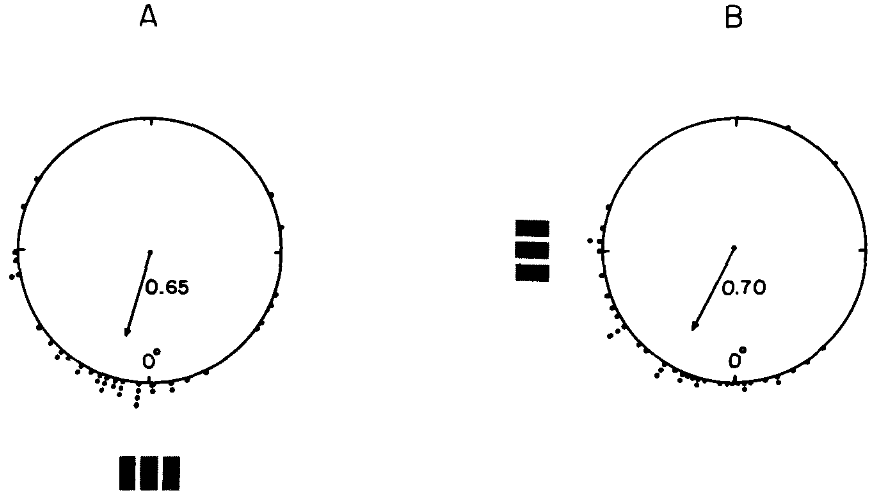

Fig. 5: Homing directions of foragers of *Odontomachus bauri* according to the position of horizontal landmarks, on a new papered floor (no canopy available). A) Unaltered landmark at 0°. B) Landmark shifted to 270°. Mean vectors are significant, and do not differ from each other ($F = 0.80$, $p > 0.25$, $df = 78$)

The following experiments tested our original observations that the ants look up more frequently when exposed to a new canopy pattern.

Using the same arrangement as for the orientation experiments described above, we first allowed foragers to get used to a control canopy pattern (stripes converging toward 0°). In each test not more than two ants were allowed to search for food in the arena. We conducted four experimental series beneath an unaltered and a 90°-rotated canopy. In each series we tested 40 ants. During the tests we counted the number of ants looking up at least once while homing.

The difference was highly significant: Beneath an unaltered canopy only 10.0 ± 4.5 ants ($\bar{X} \pm SD$) looked up, as compared with 31.2 ± 3.6 ants beneath a rotated canopy ($p < 0.001$, t-test). This suggests that ants which have lost their familiar canopy pattern scan the visual field above them with increased frequency.

In one final orientation experiment we investigated the effect that horizontal visual marks might have on the homing orientation of *O. bauri*.

We placed one plate with vertical black and white stripes (length = 6 cm) on the arena wall (5 cm from the floor), directly above the nest bridge at 0° (Fig. 1C). No canopy pattern was provided, and the ants were allowed to get used to the visual marks for one week. Using the same procedure described above, the homing of ants on fresh papered floors was registered both with the unaltered landmark at 0°, as well as with the landmark shifted to 270°.

Surprisingly the ants' homing behavior was not significantly affected by the shifting of the landmark (Fig. 5), suggesting that horizontal visual cues play no major role in the homing orientation of *O. bauri*. Such landmarks may, however, provide short range cues near the nest entrance. When the horizontal mark was shifted to 270°, ants climbed more frequently onto the bridge at that position than on any other control bridge (Table 2).

Table 2: Number of homing ants climbing on different bridges in experiments with a horizontal landmark (no canopy available). Statistical comparison made through G-test of independence. For further explanation see text

Position of landmark	Ants climbing on bridge at				p value
	0°	90°	180°	270°	
Control (0°)	37	1	0	2	< 0.025
Rotated for 270°	28	0	2	10	

Recruitment Behavior

Pilot observations in the laboratory suggested that workers of *O. bauri* are able to recruit nestmates to the foraging arena once a rich food source has been discovered. For instance, when dilute honey was offered in a glass dish (2.5 cm diameter) in the center of the arena, the number of ants entering the arena and gathering at the food source, after the first forager had discovered it, increased markedly during the following 30-min period. These results are strikingly different from those of control observations, in which an empty dish was presented (Figs. 6, 7). In both control and experimental situations (four replicates each), only one ant was in the arena when we began taking counts at 2-min intervals.

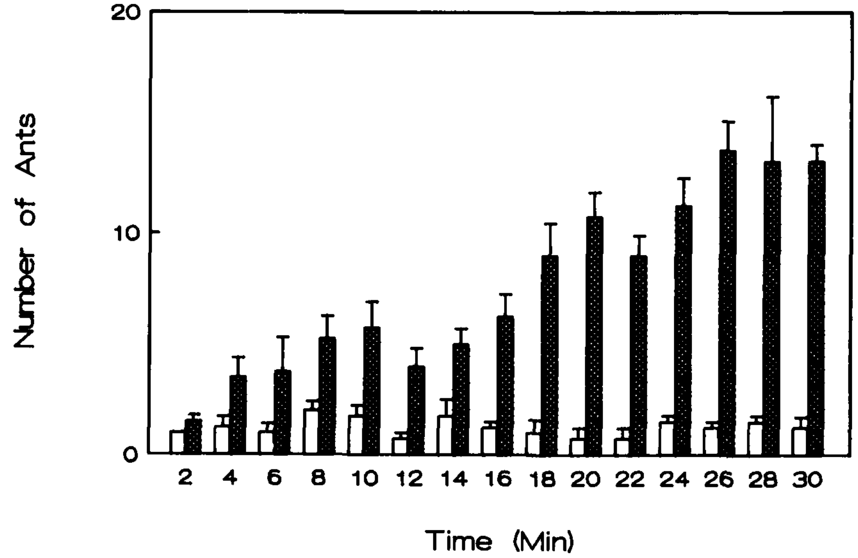

Fig. 6: Number of workers of *Odontomachus bauri* gathering at a dish containing dilute honey (hatched bars) and an empty dish (white bars) after these had been discovered by at least one forager in the center of the arena (mean and SE of four replications). Values refer to snapshot counts at 2-min intervals; only one ant was in the arena at the beginning of the observations

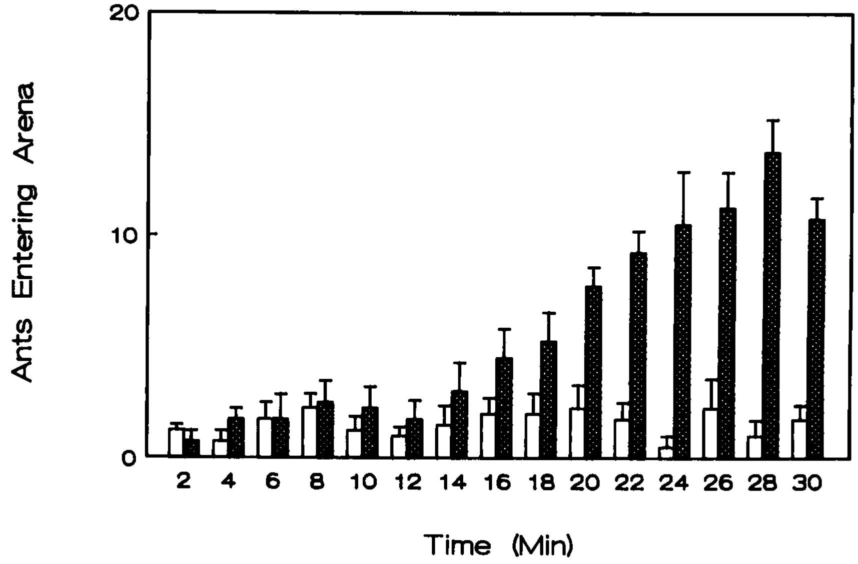

Fig. 7: Number of workers of *Odontomachus bauri* entering the arena after a dish containing dilute honey (hatched bars) and an empty dish (white bars) had been discovered by at least one forager in the center of the arena (mean and SE of four replications). Values refer to the total number of ants entering the arena within every 2 min; only one ant was in the arena at the beginning of the observations

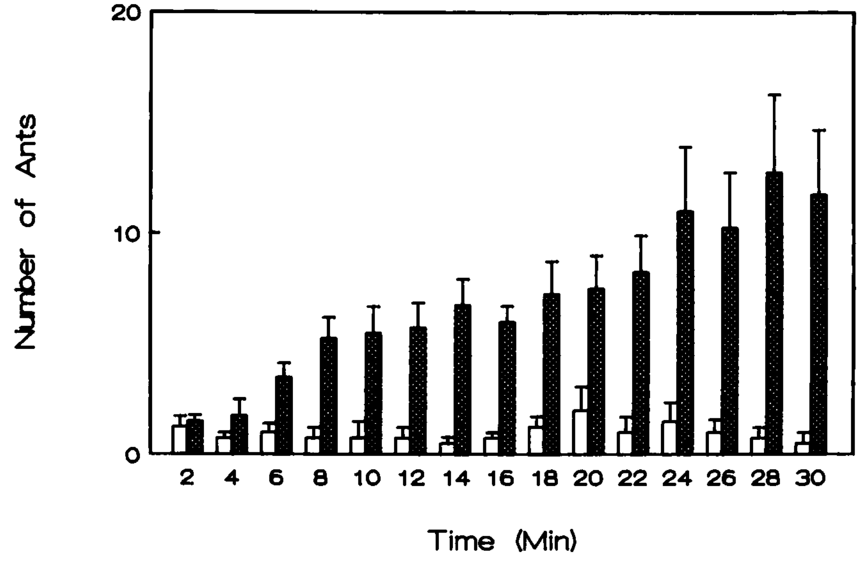

Fig. 8: Number of workers of *Odontomachus bauri* gathering at a pinned cockroach (hatched bars) and a control pin affixed to a styrofoam base (white bars) after these had been discovered by at least one forager at the center of the arena (mean and SE of four replications). Values refer to snapshot counts at 2-min intervals; only one ant was in the arena at the beginning of the observations

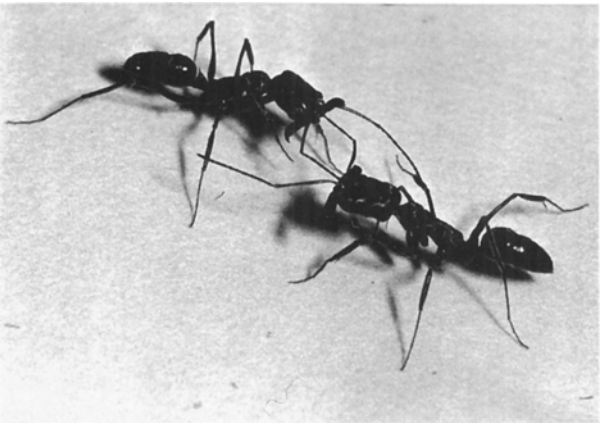

Fig. 9: Rapid antennation between workers of *Odontomachus bauri*

Similar results were obtained with insect prey. A decapitated cockroach (*Nauphoeta cinerea*) was pinned to a styrofoam base in the center of the arena (the cockroach continued to move its legs). As control we used a clean pin affixed to a styrofoam base. The procedure was the same as described above for the experiments with dilute honey. The results clearly demonstrate a recruitment effect when the insect prey, too large to be retrieved by a single forager, was offered in the arena (Fig. 8).

Our observations did not indicate, however, that during the recruitment process directional information is transmitted to the recruits. Ants entering the arena did not seem to follow chemical trails. In three subsequent experiments we arranged that the foragers entered in the center of a large rectangular arena (78 × 150 cm). In each test the food source was offered in a different direction. Although the recruitment effect was again very obvious, we now clearly observed that the recruits do not follow trails, but search randomly in the arena until they find the bait.

These results were further confirmed by tests with experimental trails. We presented at the nest exit trails (25 cm long) drawn with secretions from the poison gland, Dufour's gland, pygidial gland and hindgut contents. None of these trails elicited trail-following behavior. We also did not observe a behavioral pattern which might have indicated trail-laying behavior in *O. bauri*.

We conclude that the recruitment signal consists mainly of a stimulating signal, by which successful scouts recruit nestmates to leave the nest to search for food. It is possible that a piece of prey brought into the nest or the odor of the food alone could serve as a recruitment stimulus. We have, however, observational evidence suggesting that a successful scout ant exhibits an active recruitment behavior. When a returning forager encounters a nestmate, she frequently performs a rapid antennation behavior (Fig. 9), whereupon the nestmate responds with a similar brief antennation bout and often exhibits increased locomotory activity.

We also investigated the effect of secretions of several exocrine glands. Freshly dissected glands were crushed on filter papers or hardwood applicator sticks, and presented in the arena near the nest entrance of the *O. bauri* colony. In this experimental series we confirmed the findings obtained by WHEELER & BLUM (1973) for *O. hastatus*, *O. clarus* and *O. brunneus*: secretions from the mandibular glands elicit a strong aggressive alarm response in *O. bauri* workers. Applicator sticks contaminated with mandibular gland secretions not only provoke attraction, but also strong attack behavior in the ants. We obtained similar responses when we offered secretions from the poison gland, but observed relatively indifferent reactions in the ants toward Dufour's gland secretions.

Our comparative tests suggest that the most likely source for a chemical recruitment signal is the pygidial gland. As already shown by HÖLLDOBLER & ENGEL (1978), this gland is well developed in *Odontomachus*. It consists of two large reservoir sacs, formed by invaginations of the intersegmental membrane between the VIth and VIIth abdominal tergites, and a paired cluster of glandular cells. Crushed pygidial glands were offered on applicator sticks and presented approximately 10 cm from the nest entrance. The applicators were held approximately 1 cm above the floor, in the center of a circle of 4 cm in diameter. All ants entering the circle within a 1-min period were counted. If an ant entered the circle twice it was counted as two entries. As control we offered plain applicators, or applicators on which we had crushed the VIth abdominal tergite. Controls and pygidial gland secretions were presented in a haphazard sequence and at least 30 min elapsed between each test. The mean number of entries into the circle around the applicators with the pygidial gland secretions was 29.8 ± 15.2 ($\overline{X} \pm SD$) which is significantly higher than the value obtained with the control sticks (6.7 ± 5.8; $p < 0.001$, t-test). The ants were clearly attracted to the pygidial gland secretions. They also exhibited increased locomotory activity, but appeared less aggressive than when stimulated with mandibular gland secretions. From this circumstantial evidence we suggest that pygidial gland secretions may function as a stimulating recruitment pheromone in *O. bauri*.

Discussion

Worker ants have one or more orientation mechanisms at their disposal during foraging and homing (for review see WEHNER 1981). The various orientation mechanisms are usually not in operation simultaneously, but alternately, their sequence being dependent on spatial situations (WEHNER & MENZEL 1969; WEHNER 1981), on hierarchical order of the orientation cues available (HÖLLDOBLER 1971, 1976; ARON et al. 1988), or on experience (HARRISON et al. 1989).

Most of our knowledge concerning orientation in ants stems from studies of the phylogenetically more advanced species. Very little is known about such behavior in the phylogenetically primitive ant species, although more recent work suggests that members of the primitive subfamily Ponerinae rely primarily on chemical orientation cues during foraging and homing (for review see HÖLLDOBLER & WILSON 1990). On the other hand it has been suggested that species of the ponerine genus *Odontomachus* use predominantly visual orientation cues (JAFFE & MARCUSE 1983; DEJEAN et al. 1984), although nothing was known about the particular mechanism of visual orientation. Our laboratory studies with *O. bauri* confirm that *Odontomachus* foragers primarily use visual cues for home range orientation and we demonstrated that the canopy pattern above the ant provides the major visual orientation cue. This is the second case in which canopy orientation has been experimentally demonstrated. It was first discovered in the ponerine species *Paltothyreus tarsatus* (HÖLLDOBLER 1980). This species lives, like *O. bauri*, primarily in forested areas. Obviously, canopy orientation is well suited to the peculiarly restrictive lighting conditions of tropical forests. It now seems likely to occur also in other forest-dwelling ant species.

Successful foragers of *O. bauri* clearly transmit recruitment signals which stimulate nestmates to leave the nest and search for food, but the recruitment signal does not contain directional information about the location of the food source. Similar results were obtained with *O. ruginodis* by CARLIN & GLADSTEIN (1989). These results are in variance with the observations by JAFFE & MARCUSE (1983), who state that no recruitment occurs in *O. bauri*. Our behavioral observations suggest that recruiting ants stimulate their nestmates with short-lasting rapid antennation bouts. In addition, the bioassays of glandular contents provide circumstantial evidence that secretions of the pygidial gland serve as a chemical recruitment signal, whereas secretions from the mandibular and poison gland elicit alarm and attack behavior in *O. bauri* workers.

Pygidial gland secretions have been implicated with recruitment behavior in several other ponerine species. They serve as recruitment trail pheromones in *Pachycondyla laevigata* (HÖLLDOBLER & TRANIELLO 1980) and in some *Leptogenys* species (MASCHWITZ & SCHÖNEGGE 1977; HÖLLDOBLER unpubl.), and mediate tandem running in *Pachycondyla obscuricornis* (TRANIELLO & HÖLLDOBLER 1984). Although no trail laying or tandem running has been demonstrated in *Odontomachus*, our results suggest that secretions of the pygidial gland may function as a stimulating recruitment signal in *O. bauri* and could also serve as close range recruitment attractants near the food source.

Acknowledgements

This work was supported by a grant from the National Science Foundation (U.S.A.) no BNS 85-21575 to B. HÖLLDOBLER, and a grant from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (proc. 200512/88.9) to P. S. OLIVEIRA. We thank N. F. CARLIN for critically reading the manuscript, and S. PRATT for collecting the ants.

Literature Cited

ARON, S., DENEUBOURG, J. L. & PASTEELS, J. M. 1988: Visual cues and trail-following idiosyncrasy in *Leptothorax unifasciatus*: an orientation process during foraging. Ins. Soc. **35**, 355—366.

BATSCHELET, E. 1965: Statistical Methods for the Analysis of Problems in Animal Orientation and Certain Biological Rhythms. Am. Inst. Biol. Sci., Washington, D.C.

BHATKAR, A. & WHITCOMB, W. H. 1970: Artificial diet for rearing various species of ants. Fla. Entomol. **53**, 229—232.

BROWN, W. L., Jr. 1976: Contributions toward a reclassification of the Formicidae. Part VI. Ponerinae. Tribe Ponerini. Subtribe Odontomachini: Section A. Introduction, subtribal characters, genus *Odontomachus*. Stud. Entomol. **19**, 67—173.

CARLIN, N. F. & GLADSTEIN, D. S. 1989: The "bouncer" defense of *Odontomachus ruginodis* and other odontomachine ants (Hymenoptera: Formicidae). Psyche (Cambridge), in press.

DEJEAN, A. 1988: Memory effect on predatory behavior of *Odontomachus troglodytes* (Formicidae — Ponerinae). Behaviour **107**, 131—137.

— — & BASHINGWA, E. P. 1985: La prédation chez *Odontomachus troglodytes* Santschi (Formicidae — Ponerinae). Ins. Soc. **32**, 23—42.

— —, MASENS, D., KANIKA, K., NSUDI, M. & BUKA, M. 1984: Première approche des modalités du retour au nid chez les ouvrières chasseresses d'*Odontomachus troglodytes* Santschi (Formicidae — Ponerinae). Actes Coll. Ins. Soc. **1**, 39—47.

EVANS, H. C. & LESTON, D. 1971: A ponerine ant (Hym., Formicidae) associated with Homoptera on cocoa in Ghana. Bull. Ent. Res. **61**, 357—362.

FOWLER, H. G. 1980: Populations, prey capture and sharing, and foraging of the Paraguayan ponerine *Odontomachus chelifer* Latreille. J. Nat. Hist. **14**, 79—84.

HARRISON, J. F., FEWELL, J. H., STILLER, T. M. & BREED, M. D. 1989: Effects of experience on use of orientation cues in the giant tropical ant. Anim. Behav. **37**, 869—871.

HÖLLDOBLER, B. 1971: Homing in the harvester ant *Pogonomyrmex badius*. Science **171**, 1149—1151.

— — 1976: Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex*. Behav. Ecol. Sociobiol. **1**, 3—44.

— — 1980: Canopy orientation: A new kind of orientation in ants. Science **210**, 86—88.

— — & ENGEL, H. 1978: Tergal and sternal glands in ants. Psyche (Cambridge) **85**, 285—330.

— — & TRANIELLO, J. F. A. 1980: The pygidial gland and chemical recruitment communication in *Pachycondyla* (= *Termitopone*) *laevigata*. J. Chem. Ecol. **6**, 883—893.

— — & WILSON, E. O. 1990: The Ants. Harvard Univ. Press, Cambridge, in press.

JAFFE, K. & MARCUSE, M. 1983: Nestmate recognition and territorial behaviour in the ant *Odontomachus bauri* Emery (Formicidae: Ponerinae). Ins. Soc. **30**, 466—481.

MASCHWITZ, U. & SCHÖNEGGE, P. 1977: Recruitment gland of *Leptogenys chinensis*: a new type of pheromone gland in ants. Naturwissenschaften **64**, 589—590.

SCHEMSKE, D. W. 1982: Ecological correlates of a neotropical mutualism: ant assemblages at *Costus* extrafloral nectaries. Ecology **63**, 932—941.

TRANIELLO, J. F. A. & HÖLLDOBLER, B. 1984: Chemical communication during tandem running in *Pachycondyla obscuricornis* (Hymenoptera: Formicidae). J. Chem. Ecol. **10**, 783—794.

WEHNER, R. 1981: Spatial vision in arthropods. In: Handbook of Sensory Physiology. Vol. VII/6C. (AUTRUM, H., ed.) Springer-Verlag, Berlin, Heidelberg, New York, pp. 287—616.

— — & MENZEL, R. 1969: Homing in the ant *Cataglyphis bicolor*. Science **164**, 192—194.

WHEELER, J. W. & BLUM, M. S. 1973: Alkylpyrazine alarm pheromones in ponerine ants. Science **182**, 501—503.

Received: May 30, 1989

Accepted: July 31, 1989 (W. Wickler)