

Interspecific Trail Following and Commensalism Between the Ponerine Ant *Gnamptogenys menadensis* and the Formicine Ant *Polyrhachis rufipes*

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Gnamptogenys menadensis (subfamily Ponerinae) foragers use chemical trails to home to their nests. Although prey capture and retrieval are generally performed solitarily, trails seem to enhance foraging to areas rich in prey or to sugar sources. Trail laying and following are most conspicuous during nest migration. These trails are laid down by tapping the sting onto the substrate. In laboratory tests, only extracts from the Dufour's gland were readily followed. Workers of *Polyrhachis rufipes* (Formicinae) use the trails of *G. menadensis* to gain access to otherwise nonavailable sugar sources. When they encounter *Gnamptogenys* foragers, *P. rufipes* workers show a typical aggressive antennal boxing, to which *Gnamptogenys* reacts with a submissive behavior. This is the first report of commensalism between a ponerine and a formicine ant.

KEY WORDS: Ponerinae; Formicinae; interspecific interactions; trails; recruitment.

INTRODUCTION

All ponerine ants hunt arthropods as a major part of their diet (Peeters, 1997). Some species are solitary predators, while others have elaborate systems of recruitment. Recruitment can occur with or without cooperation in prey capture and retrieval, depending on whether the ants hunt large prey items or clusters

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of small prey. Simple and complex hunting strategies occur in different species irrespective of their phylogenetic relationships (Pecters and Crewe, 1987). Trail-following behavior is described in several ponerines, but the glandular origin of the trail pheromone is known in only a few species [pygidial, sternal, and venom glands (Hölldobler and Wilson, 1990); Dufour's gland (Bestmann *et al.*, 1995)]. Thus far, the trail substances have been chemically identified in only four ponerine ants (Billen and Morgan, 1998).

Trail-following behavior is described in several neotropical species of *Gnamptogenys*. Field observations of *G. bispinosa*, *G. concinna*, and *G. regularis* show that recruitment leads to coordinated attacks on large prey or prey nests, while in *G. hartmani*, trail recruitment during nest emigration seems to exist (Latke, 1995). Pratt (1994) found evidence of trail recruitment in *G. hornii* by offering baits pinned to the floor of the arena. However, in neither of these species has the existence of a trail pheromone or its anatomical origin been empirically demonstrated.

In the arboreal *Gnamptogenys menadensis*, colonies with either sexually reproducing workers (gamergates) or queens occur. Foragers hunt arthropods on the vegetation, while occasional sugar sources can also be exploited (Gobin *et al.*, 1998). While foraging, *Gnamptogenys* workers seem to follow trails. Workers of the arboreal formicine ant *Polyrhachis rufipes* frequently interacted with *G. menadensis* foragers on these trails. In this paper, we present data on the origin of trail substances in both species, with special attention to the interspecific interactions.

MATERIALS AND METHODS

Field observations were made in January 1994, February 1995, and March 1996 in the Karaenta Nature Park, South Sulawesi, Indonesia. Complete colonies of *Gnamptogenys menadensis* (Mayr) and nests of *Polyrhachis rufipes* F. Smith were collected and transported to Belgium. Colonies were kept in plaster nests at $25.5 \pm 2^\circ\text{C}$ and $75 \pm 15\%$ humidity under a 12:12 day:night rhythm. Artificial trail experiments were performed with ants collected in 1995 and 1996. Glandular hexane extracts and hexane blanks were made and presented to workers on circular trails in an arena as described by Pasteels and Verhaeghe (1974). All contacts with the trail were counted, together with the distance (cm) the ant moved along the trail during every contact. Each ant was given 2 min in the arena, with a maximum of 10 contacts counted. Average distances followed were calculated per ant and per trail and analyzed using an ANOVA on rank-transformed values and a Tukey HST test (unequal N) for multiple post hoc comparison. Chemical analyses using the solventless technique (Morgan and Wadhams, 1972) were performed on a HP 5890 gas chromatograph (nonpolar column) connected to a HP5970B mass selective detector. Samples were run at

30°C initial temperature for 3 min, raised at a rate of 7°C per min to 280°C, and kept for 10 min at this final temperature.

RESULTS

In their natural habitat, foragers of *G. menadensis* returning with prey found their way with few mistakes in the labyrinth of branches from the shrubs and trees in which they live. Several workers were seen returning to their nests from distances of up to 10 m. Whenever they came to a junction, they inspected the surface with their antennae before continuing. If they chose the wrong direction, they always moved back after just a few centimeters. Some prey-carrying foragers frequently tapped their sting onto the branch surface when homing to the nest. This trail enhanced foraging to certain areas of shrubs, such as accumulations of detritus. Several motionless foragers were often found on sunny leaves, stalking prey. Even when many foragers were near each other, there was very little cooperation in prey capture and prey retrieval. An occasional bystander could assist, but this never lasted more than a few seconds. *G. menadensis* could gain access to sugar sources by biting and thus damaging the plant material (Gobin *et al.*, 1998).

Trail recruitment was even more conspicuous when workers were forced to migrate to a new nest site. Workers leaving the nest regularly tapped the substrate with their sting to lay a trail, which they used to return to the nest. As soon as a suitable cavity was found, returning workers reinforced this trail through intensive tapping. Several workers then started following the trail back and forth between the two sites, transporting brood to the new nest site.

When artificial trails with extracts of several abdominal glands were presented to workers of *G. menadensis*, the ants followed Dufour's gland extract significantly more than other gland extracts or blanks (Fig. 1). This is in accordance with the field observations of sting-tapping, since the Dufour's gland opens together with the venom gland duct through the sting (Billen, 1987). Males never followed artificial trails that were readily followed by workers, nor did the males follow any other glandular extracts from workers.

The slight trail following response recorded with pygidial gland extract can be explained by its short-range recruitment qualities. Whenever attacked or manipulated, *G. menadensis* workers smear the strong-smelling, hydrophobic contents of the pygidial gland on the aggressor or forceps. This possibly is a defensive repelling substance, but also serves to attract nearby nestmates to the aggressor. When pygidial gland reservoirs are squeezed between forceps in the foraging arena, nearby ants will approach with open mandibles. Nevertheless, Dufour gland extracts elicit a significantly stronger trail-following response than pygidial gland extracts (Fig. 1).

We frequently observed workers of the formicine ant *P. rufipes* in the

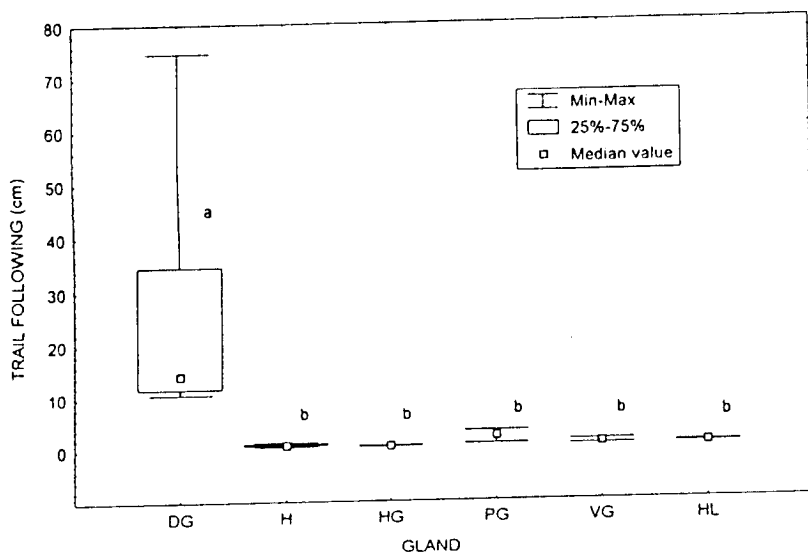


Fig. 1. Trail following response of *Gnamptogenys menadensis* workers to artificial trails of extracts of Dufour's gland (DG; $N = 32$); hindgut (HG; $N = 10$); pygidial gland (PG; $N = 22$); venom gland (VG; $N = 16$) and hind legs (HL = 10) compared to pure hexane (H; $N = 27$). The response to Dufour's gland extract differs significantly from hexane ($P > 0.01$), while other gland extracts did not differ significantly from hexane (significant differences indicated by different letters on graph). Significance was calculated with ANOVA on rank-transformed values and a Tukey HST-test (unequal N) for multiple post hoc comparison.

vicinity of nests and foraging trails of *G. menadensis* ($N = 40$). A nest of *P. rufipes* was situated less than 30 cm from a *Gnamptogenys* nest on three occasions. *P. rufipes* is slightly larger than *G. menadensis*. Apart from the spines, both species are very similar in appearance, especially due to the pock-marked surface of the cuticle of head, thorax, and node. In a face-to-face encounter, *G. menadensis* workers will attack, bite, and attempt to sting *P. rufipes*. Sometimes they succeed in killing the *Polyrhachis*, after which they will carry it to the nest as any other prey. During our field observations it was clear that the more agile *P. rufipes* avoided frontal encounters. They will, however, frequently perform a very specific attack on *G. menadensis* foragers. A worker of *Polyrhachis rufipes* will approach a *G. menadensis* worker from behind and climb on top of it while grabbing it underneath the thorax with the forelegs (Fig. 2), after which bouts of quick antennation are directed toward the head, mandibles, and antennae of the seized *Gnamptogenys*. Occasionally, *P. rufipes* will repeatedly tap its abdomen on that of *G. menadensis*, a behavior similar to the alarm tapping behavior seen in other *Polyrhachis* species. *G. menadensis* reacts to these attacks by lowering the abdomen and pulling the antennae backward,

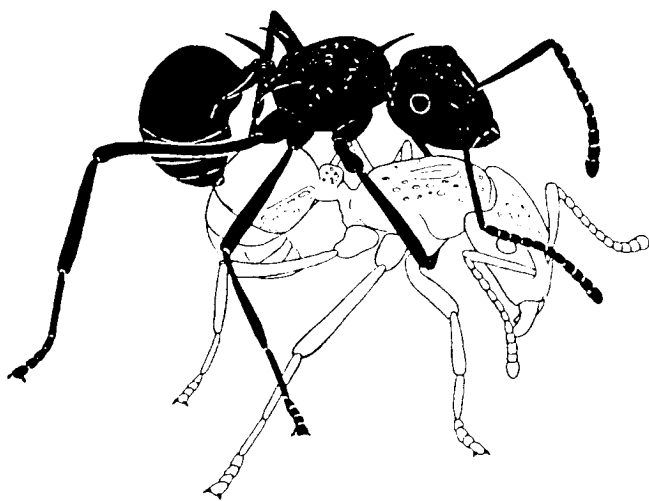


Fig. 2. Aggressive interaction of *Polyrhachis rufipes* (black) on *Gnamptogenys menadensis*. In this posture, *P. rufipes* will box with its antennae at the head of *G. menadensis*. Note the *Polyrhachis* forelegs grabbing *Gnamptogenys* under the thorax.

which might be considered submissive. On the other hand, *G. menadensis* will regularly open its mandibles in threat while in this lowered posture.

P. rufipes workers often walked onto the organic material lining the entrance of *G. menadensis* nests, performing this specific behavior on foragers leaving and entering the nest. We also recorded a high incidence of interactions near sugar sources exploited by *G. menadensis*. *P. rufipes* workers were never seen damaging plant material themselves but licked at wounds created by *Gnamptogenys*. *G. menadensis* foragers could, nevertheless, still continue to feed in the near-vicinity. *P. rufipes* never stole prey items from returning foragers of *G. menadensis* in the field, nor eggs, larvae, or cocoons carried by *Gnamptogenys* workers during laboratory trials. We often observed *P. rufipes* workers leaving the *Gnamptogenys* nest area, following the identical route of the *Gnamptogenys* foragers, suggesting that they followed their trails to locate resources.

In artificial trail tests, *P. rufipes* workers will follow extracts originating from the hindgut, which is a common trail pheromone source in formicine ants (Hölldobler and Wilson, 1990). However, they will also readily follow extracts of *G. menadensis* Dufour's gland (significant difference from blank controls, $P < 0.005$). *G. menadensis* workers also followed an extract of *P. rufipes* hindgut. Preliminary chemical analysis of the pheromone source in each species revealed that both contain the same range of hydrocarbons (C_{13} – C_{19} ; Fig. 3). We did not locate the exact positions of double bonds in these compounds. The Dufour's

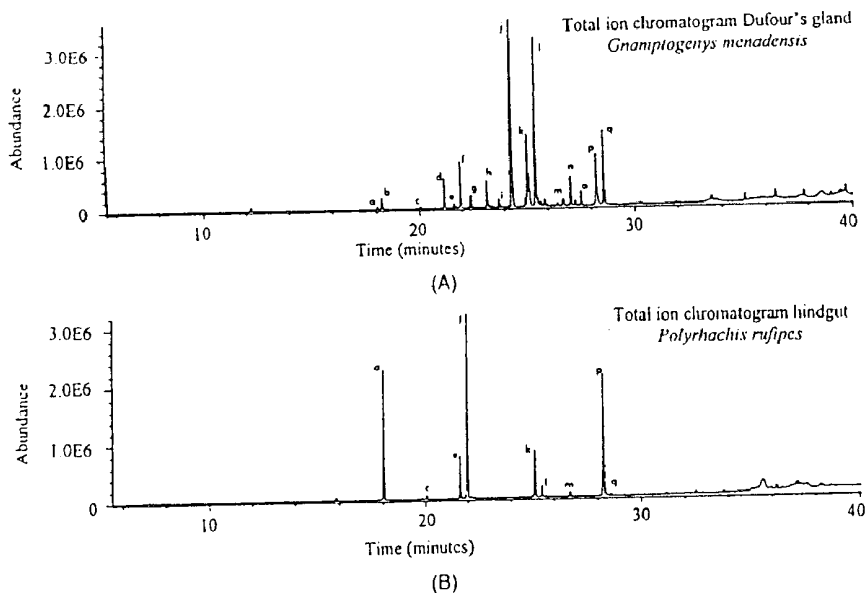


Fig. 3. Gas chromatogram of *Gnamptogenys menadensis* Dufour's gland (A) and *Polyrhachis rufipes* hindgut (B). Compounds are as follows: (a) tridecane, (b) terpene, (c) tetradecane, (d) β -farnesene, (e) pentadecene, (f) pentadecane, (g) terpene, (h) β -homofarnesene, (i) hexadecane, (j) β -bishomofarnesene, (k) heptadecene, (l) heptadecane, (m) octadecene, (n) octadecane, (o) aldehyde, (p) nonadecene, and (q) nonadecane.

glands of *Gnamptogenys* contain in addition a series of β -farnesenes, all of which have been found in other ant species. Furthermore, there is an unidentified terpene (figure 3A) and a long chain aldehyde, probably hexadecanal. None of these were detected in *P. rufipes* hindguts, (figure 3B). At present, we do not know which of the substances they have in common might be the active trail substance.

DISCUSSION

The use of trail pheromones during foraging or nest migration is documented in three ponerine tribes (Peeters and Crewe, 1987; Peeters, 1997). In ponerine ants, a wide range of hunting strategies exists, from solitary hunting without recruitment to coordinated attacks with advanced chemical recruitment. The colony size of a species appears to be associated with its hunting strategy (Beckers *et al.*, 1989), although causality is by no means clear in this context. In *G. menadensis*, which have rather small colonies [average, 100 workers (Gobin *et al.*, 1998)], prey capture and prey retrieval are generally performed by individual workers. This is in agreement with the small prey sizes brought back by the foragers. Therefore, foraging trails might serve as homing cues.

Occasionally, trails can enhance foraging of solitary hunters to certain areas where prey might be abundant. Since trophallaxis is absent in this species (Gobin *et al.*, 1998), recruitment of nestmates to sugar sources can also be adaptive. Additionally, in species with frequent nest migration, we might expect the evolution of a well-developed recruitment system. In *G. menadensis*, nest migration is sometimes associated with temporal polydomy and gamergate colonies reproduce by budding (Gobin *et al.*, 1998), which is consistent with the observation that trail recruitment is most obvious during nest emigration.

Gnamptogenys menadensis and the formicine *Polyrhachis rufipes* follow each other's trails, although their respective trail pheromones originate in different glands. Interspecific trail following has been described between several higher ant species (Hölldobler and Wilson, 1990). Except for the social parasitic species, the species which produces the trail shows certain forms of aggressive or expelling behavior toward the intruding species (Kaudewitz, 1955; Baroni Urbani, 1969; Wilson, 1965; Swain, 1980). The guest species' response to this aggression is either immobilization or avoidance behavior. *G. menadensis* workers will attack *P. rufipes* workers and can kill them. *P. rufipes* is more agile and can easily avoid this aggression. However, *P. rufipes* workers will actively approach and dominate *Gnamptogenys* workers by grabbing them from behind and performing antennal boxing. As in many queenless ponerine ants, workers of *G. menadensis* use ritualized antennal boxing during intranidal dominance interactions to regulate reproduction (Gobin *et al.* in preparation). Subordinate workers will often respond to this by lowering the body and moving the antennae backward. Antennal boxing of *P. rufipes* will also immobilize a *G. menadensis*, but it is not clear if these interactions will progressively reduce the aggressiveness of the ponerine ant toward the *Polyrhachis* workers using its trail. Why, then, does *P. rufipes* continue to seek out *G. menadensis* workers and dominate them? It is possible that through these antennations, *P. rufipes* can probe whether returning *Gnamptogenys* foragers have recently fed on sugar secretions, maybe by remnants of sugar on the mouthparts. With this information they can then decide to start following the trails of *Gnamptogenys*. It is equally possible that *Polyrhachis* workers benefit from the predator-repelling substances (pygidial gland) and stinging capacities of *Gnamptogenys* by mimicking the latter. The pock-marked appearance of the *Polyrhachis* cuticle is exceptional for this genus in the oriental tropics (F. Ito, personal communication) but very similar to that of *G. menadensis*.

Reports on interactions of ponerine ants with ants of other subfamilies are rare. When collecting species of the *Polyrhachis viehmeyeri* species group (Formicinae), Kohout (1990) found a *Rhytidoponera* sp. nesting under the same rocks with four *Polyrhachis* spp. There exists a single report of *Odontomachus affinis* nesting parabiotically with *Monacis rufescens* (Mann, 1912). The interactions of *P. rufipes* and *G. menadensis*, expressed in trail sharing and ritualized

interactions, are the first account of commensalism between a formicine and a ponerine ant. This association has a distinct advantage for *P. rufipes*, giving it additional access to sugar sources. However, we could not detect a clear disadvantage for *G. menadensis*, since it is not certain that the interactions with *P. rufipes* reduce their access or yield from this resource.

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