# Ecology and behavior of *Gnamptogenys horni* (Formicidae: Ponerinae)

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## Summary

In order to examine social behavior in the little-studied ponerine ant genus *Gnamptogenys*, detailed observations were made on captive colonies of *G. horni*. Compilation of a behavioral repertory gave evidence of age-based division of labor, with old ants more likely to forage and young ants more likely to tend brood. Workers were observed to line the walls of their nests with pieces of old cocoons, a behavior referred to as wallpapering and previously known from only one other ant species. Evidence was obtained for the use of trail recruitment pheromones in foraging and in nest-moving. Examination of prey remains in natural nests indicated that *G. horni* feeds principally on a wide variety of ants, but also on other arthropods.

## Introduction

*Gnamptogenys horni* is a small ant of the ponerine tribe Ectatommini found in moist tropical forests from Panama to Bolivia. The genus as a whole is widespread in the Indo-Australian region and in the New World from Texas to Argentina. *G. horni* forms small colonies, rarely exceeding 200 individuals, which typically nest in rotten wood or other organic material on the forest floor (Brown, 1958; Lattke, 1990). Although there is some evidence that it is a specialized predator on ants (Hölldobler and Wilson, 1990), Lattke (1990) reports that its diet also includes beetles, pseudoscorpions and other arthropods. Like most members of the genus, it is relatively rare and cryptic, hence little else is known of its behavior and ecology. In order to shed more light on the natural history of this large but little-studied genus, I report here on observations of *G. horni* in which I was able to examine many aspects of social behavior, including recruitment communication, diet and division of labor.

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**Materials and methods**

The studies were conducted at the Smithsonian Tropical Research Institute on Barro Colorado Island, Republic of Panama, during the rainy season months of July and August, 1987. Vegetation at the collection site consisted of scrubby young tropical moist forest (Foster and Brokaw, 1982). Colonies were transferred after collection to observation nests consisting of small plastic petri dishes (9 cm diameter) floored with plaster. A large glass cover slip resting 2 to 3 mm above the floor on small pellets of aluminum foil gave the ants an adequate nesting site open to behavioral observation. The area outside the glass served as a foraging arena. The nest was kept moist by regularly sprinkling water on the plaster floor. A small amount of soil was provided as additional nest-building material. Voucher specimens from these observation colonies were deposited in the Museum of Comparative Zoology at Harvard University and in the Invertebrate Museum at the University of Panama.

Behavioral observations were made on two colonies (1 and 3) through a dissecting microscope at $120 \times$ to $250 \times$ magnification. In order to compile a behavioral catalog, the nest interior was repeatedly scanned during observation sessions lasting thirty-five to seventy-eight minutes. On each scan I noted any acts besides walking or standing, as well as the age of the actor. A total of 8.8 hours of data were taken on colony 1 and 7 hours on colony 3. Observations were made between 0900 and 2200, but most were made in the afternoon and evening. Colony 1 was observed from 18 to 20 July 1987 and colony 2 from 9 to 10 August 1987.

In order to examine age-based division of labor I identified young workers on the basis of their pale coloration. Young ants could be reliably distinguished from fully pigmented adults up to ten days after eclosion. The absolute frequencies of behaviors by young and old ants were compared via a $\chi^2$ test of independence. This and other statistical tests were performed on StatView II™. Tests of recruitment are discussed in the relevant sections of the results.

**Results**

*I. Nest sites, colony population*

Seven complete colonies were found nesting on the forest floor, including six in old *Dipteryx sp.* seed husks 4–5 cm in length and one in a small rotten tree branch. The husk nests had only one very inconspicuous entrance. When split open, they revealed a single hollow cavity, sometimes further confined by walls of soil. These walls also contained pieces of arthropod exoskeletons, presumably the remains of prey.

Two-colonies were censused and used for subsequent behavioral observations. Colony 1 had nine queens, sixty-seven to seventy-five fully pigmented workers, thirteen to twenty callow workers, four to eight eggs, thirty-five to fifty-five larvae, and thirteen to fourteen pupae. Colony 3 had one queen, seventeen to eighteen fully pigmented workers, twenty-two to twenty-six callow workers, thirty to forty eggs, fifteen to twenty-five larvae, and twenty-five to thirty pupae. All queens were dealate and distinctly larger than workers. The population ranges reflect variation among

daily counts over the two to three days needed for behavioral observations. This variation may reflect both imprecision in the counts and actual daily changes in population.

## II. Behavioral repertory

Table 1 gives the absolute frequencies of all behaviors observed in colonies 1 and 3. Most of these are familiar from other behavioral studies of ants, but some require further description.

*Help pupation, help adult eclosion:* Workers piled pieces of soil and debris on spinning larvae, presumably to provide them with a framework on which to build

**Table 1.** Number of times each behavior was performed by young workers, by old workers and by queens

| Behavior | | Colony 1 | | | Colony 3 | | |
|---|---|---|---|---|---|---|---|
| | | young | old | queens | young | old | queen |
| Egg Care | Lick egg | 0 | 5 | 0 | 11 | 11 | 0 |
| | Antennate egg | 0 | 0 | 0 | 0 | 0 | 0 |
| | Handle egg | 10 | 24 | 1 | 21 | 20 | 0 |
| Larval Care | Lick larva | 86 | 209 | 4 | 45 | 28 | 1 |
| | Antennate larva | 0 | 0 | 0 | 0 | 0 | 0 |
| | Handle larva | 25 | 83 | 3 | 41 | 24 | 0 |
| | Feed larva | 0 | 1 | 0 | 0 | 0 | 0 |
| Pupal Care | Lick pupa | 2 | 2 | 0 | 8 | 6 | 0 |
| | Antennate pupa | 0 | 0 | 0 | 1 | 1 | 0 |
| | Handle pupa | 1 | 2 | 0 | 11 | 13 | 0 |
| | Help pupation | 0 | 0 | 0 | 0 | 0 | 0 |
| | Help eclosion | 0 | 0 | 0 | 6 | 5 | 0 |
| Social Grooming | Groom worker | 5 | 37 | 0 | 22 | 35 | 0 |
| | Groom queen | 0 | 7 | 0 | 0 | 0 | 0 |
| Nest maintenance | Handle nest material | 0 | 3 | 0 | 0 | 5 | 0 |
| | Handle other material | 1 | 4 | 0 | 0 | 1 | 0 |
| | Lick nest wall | 0 | 0 | 0 | 0 | 0 | 0 |
| | Tear cocoon | 0 | 0 | 0 | 1 | 6 | 0 |
| | Wallpaper | 0 | 1 | 0 | 0 | 4 | 0 |
| Other Task | Carry worker | 0 | 5 | 0 | 0 | 1 | 0 |
| Non-task Behaviors | Self-groom | 80 | 254 | 26 | 170 | 216 | 7 |
| | Antennate queen | 0 | 0 | 5 | 0 | 0 | 0 |
| | Antennate worker | 0 | 0 | 0 | 0 | 0 | 0 |
| | Eat prey | 79 | 214 | 10 | 5 | 7 | 0 |
| | Eat brood | 0 | 0 | 0 | 3 | 0 | 0 |
| | Eat dead ant | 0 | 15 | 0 | 0 | 0 | 0 |
| | Handle food | 1 | 13 | 0 | 4 | 2 | 0 |
| | Drink | 0 | 10 | 0 | 0 | 0 | 0 |
| | Drink larval drop | 0 | 2 | 0 | 0 | 0 | 0 |
| | Antennal tip | 4 | 0 | 0 | 0 | 1 | 0 |
| | Expel infrabuccal pellet | 0 | 1 | 0 | 2 | 0 | 0 |
| Total | | 294 | 892 | 49 | 351 | 386 | 8 |

their cocoons. Eclosing callows were assisted by workers who opened the cocoon at its anterior end. The assistants then tore off the cocoon and removed the remaining pieces of pupal skin from the callow.

*Tear cocoon, wallpaper*. In natural nests, the walls near the brood area were covered with small brown spots which light microscopic examination revealed to be pieces of cocoon. In observation nests, similar pieces soon dotted the coverslip and the loose soil walls built by the workers around the coverslip's edge. The production of this coating was observed several times following adult eclosions. Within a few minutes of an eclosion, workers ripped up the old cocoon and pressed the pieces into the wet soil walls, using their mandibles and forelegs. All cocoons seemed to be used in this way, since none were ever seen in the colonies' waste areas. This behavior was referred to as wallpapering after the similar phenomenon described in *Prionopelta amabilis* (Hölldobler and Wilson, 1986).

*Feed larvae:* Workers fed larvae by placing pieces of prey directly on their mouthparts.

*Drink larval droplet:* Workers were sometimes seen drinking a liquid exuded from the posterior end of larvae. Similar behaviors have been described for other ants (LeMasne, 1953) and may serve a nutritive function.

## III. Division of labor

Queens were largely inactive, very infrequently grooming eggs or larvae. Workers showed evidence of temporal polyethism, with younger ants performing higher rates of brood care and older ants performing more nest maintenance, grooming, and foraging (Table 2). The analysis of division of labor included only those behaviors shown in Table 1 under the task categories egg care, larval care, pupal care, grooming and nest maintenance. Because foraging was not directly observed (observations were confined to the nest interior), I estimated foraging rates in colony 3 by occasionally surveying the foraging arena and noting the number and age of ants there. No estimate of foraging activity was made for colony 1. However, additional evidence for the absence of foraging by young workers was seen in recruitment experiments reported below. Only fully pigmented ants foraged and responded to recruitment in these experiments.

**Table 2.** Observed frequencies of task behaviors by young and old workers of two *G. horni* colonies, and expected frequencies (italics) based on the assumption that both age groups are equally likely to perform each task. Observed and expected frequencies differ significantly in both colonies ($\chi^2$-test of independence)

|          | Age   | Brood Care | Grooming | Nest Care | Foraging | $\chi^2$   |
|----------|-------|------------|----------|-----------|----------|------------|
| Colony 1 | Young | 124        | 5        | 1         | –        | 8.00       |
|          |       | *(115)*    | *(13)*   | *(2)*     |          | (p < 0.02) |
|          | Old   | 326        | 44       | 8         | –        |            |
|          |       | *(335)*    | *(37)*   | *(7)*     |          |            |
| Colony 3 | Young | 144        | 22       | 1         | 0        | 25.30      |
|          |       | *(128)*    | *(29)*   | *(9)*     | *(2)*    | (p < 0.001)|
|          | Old   | 108        | 35       | 16        | 4        |            |
|          |       | *(124)*    | *(28)*   | *(8)*     | *(2)*    |            |

## IV. Diet

Workers in observation nests retrieved and ate a wide variety of freshly killed food, including amphipods, collembola, small centipedes, isopods, termites, crickets, *Pheidole sp*. brood, and small annelids. They showed no interest in sucrose solution. Examination of arthropod remains in the middens of natural nests also suggested a broad range of prey items. Among the identifiable items were mites, termites and several beetles, including curculionids and a staphylinid. Most remains were of ants, including the arboreal genera *Eucryptocerus* and *Azteca* and the following ground-dwelling ants: *Neivamyrmex, Solenopsis, Pheidole, Carebarella, Pachycondyla, Seric-omyrmex, Wasmannia, Strumigenys, Atta, Gnamptogenys* (not *horni*) and *Erebomyrma panamensis*.

## V. Recruitment

Evidence of recruitment to food was sought by offering baits (termites, chironomid flies or brood of the ant *Ectatomma ruidum*) pinned to the plaster floor 3.5 to 4 cm from the nest entrance. A forager typically discovered the bait within a few minutes. After biting and stinging it and struggling to move it for several minutes, she returned to the nest, tapping the tip of her gaster against the substrate. On returning to the nest, she remained inside for less than five seconds, running around the entrance area and briefly antennating workers. Fully pigmented workers responded to this antennation with restlessness and excitement, but callow ants showed no response. Many of the aroused workers left the nest and followed the same route taken by the discoverer to reach the bait. The discoverer also returned to the bait, often tapping her gaster against the substrate as before.

Seven such apparent recruitment events were closely observed in the laboratory. Figure 1 depicts the effect of trail-laying on the population of workers at the bait in
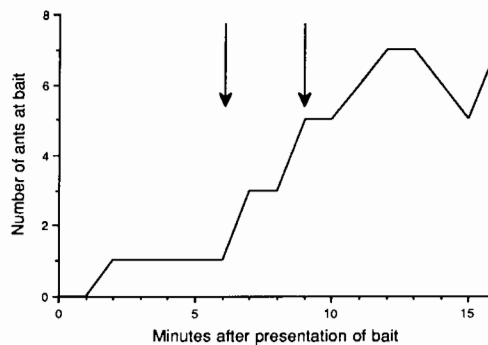


**Figure 1.** Recruitment to food by *Gnamptogenys horni*. A freshly-killed chironomid fly was pinned to the arena floor 3.5 cm from the nest entrance. One worker discovered the bait within two minutes and returned to the nest, laying a recruitment trail, four minutes later (left arrow). This and a subsequent trail (right arrow) were followed by a dramatic increase in the number of ants at the bait

one of these events. In order to determine whether the trail-laying actually had an effect on the number of ants leaving the nest to forage, I took control observations for five to ten minutes, before setting out the bait, of the number of ants exiting each minute. After the bait was presented and a trail-layer had entered the nest, the number of ants leaving the nest in the next two minutes was recorded. For the test, the largest number of ants exiting in any two-minute period during the control observations was compared with the number exiting two minutes after the return of the trail-layer. The figures were significantly different (Pre-trail: $1.6 \pm 0.79$ ants, Post-trail: $5 \pm 1.8$ ants, $p < 0.01$, Mann-Whitney U, figures give mean $\pm$ standard deviation).

In order to determine whether recruitment actually increased the number of ants finding the bait, the rate of discovering food before trail-laying was compared with the rate after a trail had been laid. The number of discoverers before recruitment was approximated by the largest number of ants seen at the bait at one time before the first trail was laid. The number of discoverers after recruitment was approximated by the largest number of ants seen at the bait at one time after trail-laying minus the number of discoverers before trail-laying. The rates were simply these numbers divided by the amount of time between bait presentation and trail-laying (pre-trail) and the amount of time between trail-laying and the end of the experiment (post-trail). These figures were also significantly different (Pre-trail: $0.22 \pm 0.07$ ants/minute, Post-trail: $0.78 \pm 0.19$ ants/minute, $p < 0.01$, Mann-Whitney U, figures give mean $\pm$ standard deviation).

There was also evidence of recruitment in nest movement. When a colony was separated into two parts during the set-up of an observation nest, trail-like traffic developed between the two groups. Workers carried brood from the smaller group to the larger one, evacuating the smaller group within five minutes. Ants were seen tapping their gasters on the substrate as they walked between the two areas.

### Discussion

Wallpapering of brood areas with old cocoons has been noted only once before, in *Prionopelta amabilis*, where it appears to function in reducing humidity near the pupae (Hölldobler and Wilson, 1986). It may serve the same function here, since the nests are quite damp and the wallpapering is found predominantly in the brood area. As *P. amabilis* is an amblyoponine and therefore not closely related to *G. horni*, closer investigation may reveal this behavior to be relatively widespread, at least among the Ponerinae.

The readiness of workers in laboratory nests to eat and recruit to a variety of arthropod food sources, as well as the presence of diverse arthropod remains in the kitchen middens of natural nests, indicates that *G. horni* is not a specialist predator on ants, as suggested by Hölldobler and Wilson (1990). However, prey remains in natural nests included a preponderance of ants, in agreement with the observations of Lattke (1990) in Venezuela. *G. horni* may forage primarily on ants while also hunting or scavenging other arthropods. If ant prey are taken in raids on nests, rather than singly while foraging, *G. horni*'s trail recruitment abilities could be useful in

summoning an adequate force for attacking these well-defended and concentrated food sources.

*G. horni* has a pattern of temporal polyethism typical of social insects generally, with young workers concentrating on brood care and old workers on nest maintenance and foraging (Hölldobler and Wilson, 1990). Nonetheless, the behavioral profiles of young and old ants overlap extensively. In particular, old ants perform significant amounts of brood care, although it makes up a smaller proportion of their total activity than is the case with young ants. This overlap may in part reflect the crudeness of pigmentation as a cue for age. The fully pigmented class may include both younger ants focusing on brood care and older ants dedicated to nest maintenance and foraging.

Overlap between caste profiles could also reflect behavioral flexibility of workers and interindividual variability within castes, features which may have functional significance in the organization of labor in social insect colonies (Calabi, 1989). Quantitative studies of age polyethism in ponerines are few, but they have generally reported broad, overlapping age caste profiles or marked interindividual variability within castes: *e.g., Ectatomma ruidum* (Corbara et al., 1989), *Megaponera foetens* (Villet, 1990), *Platythyrea schultzei* (Villet, 1991), *Ponera pennsylvannica*, (Pratt, 1994), and *Prionopelta amabilis* (Hölldobler and Wilson, 1986). Clarification of the nature of polyethism in *G. horni*, and in ponerines generally, would benefit from further studies using individually marked ants of known age.

## Acknowledgements

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