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***Gnamptogenys hartmani* Wheeler (Ponerinae: Ectatommini): an agro-predator of *Trachymyrmex* and *Sericomyrmex* fungus-growing ants**

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Abstract The fungus gardens of fungus-growing ants are a potentially valuable resource for exploitation by natural enemies, but few of these antagonistic interactions have been studied. Here we describe key aspects of the behavioral ecology of *Gnamptogenys hartmani* (Ponerinae: Ectatommini), a specialized “agro-predator” of *Trachymyrmex* and *Sericomyrmex* fungus-growing ants in Panama. Raiding columns of *G. hartmani* attack and usurp nests with remarkably little effort: a few intruding workers are sufficient to cause panic among the attine ants and make them abscond from the nest. Both *G. hartmani* larvae and adults consume the fungus and the host brood, after which the colony migrates to a new fungus-growing ant nest discovered by scouting workers. The morphology of the *G. hartmani* larval mouthparts is similar to that of *Gnamptogenys* species with a non-fungal diet. However, we suggest that the presence of long spinules on the larval mandibles in the genus *Gnamptogenys*, comparable to those found in attine larvae, may have pre-adapted *G. hartmani* to fungus eating. *G. hartmani* workers do not actively maintain or modify fungus gardens, which makes them less efficient exploiters than *Megalomyrmex*, the only other agro-predatory ant species known so far.

Introduction

Attine ants (Myrmicinae: Attini) are obligately dependent on cultivating a mutualistic fungus for food. Their fungus gardens constitute a valuable resource that could be exploited by other species. Recent studies have discovered several highly specialized exploiters of attine colonies, such as the parasitic fungus *Escovopsis* (Currie et al. 1999,

2003) and the social parasite *Acromyrmex insinuator* (Bekkevold and Boomsma 2000), but remarkably few cases of other ants exploiting fungus gardens are known. In particular the mutualistic fungi of the higher attines, with their specialized food-bodies (gongylidia) that are rich in glycogen and amino acids (Kermarrec et al. 1986), should be attractive resources for opportunistic or specialized usurper ants. However, at present only ants in the *Megalomyrmex silvestrii* group are known to be trophic parasites of *Apterostigma*, *Cyphomyrmex*, *Trachymyrmex*, and *Sericomyrmex* attine ants (Adams et al. 2000). In most *Megalomyrmex* species described, the parasite workers cohabit peacefully with the attine ants within or adjacent to the fungus gardens. Recently a new *Megalomyrmex* species was described that aggressively usurps colonies of *Cyphomyrmex* and feeds on the fungus and the host brood (Adams et al. 2000). Adams et al. coined the term “agro-predator” to describe this species, which is thought to migrate to new host colonies after depleting the fungus.

In this article we give the first description of key aspects of the behavioral ecology of a second agro-predatory ant species, *Gnamptogenys hartmani* Wheeler. *G. hartmani* ranges from the southern United States to Brazil (Lattke 1995) and has been reported to be a predator of *Trachymyrmex* species (Brown 1961; Echols 1964; Lattke 1995). Echols (1964) reported that *G. hartmani* occupied nests of *T. septentrionalis* in Louisiana and fed on the attine brood, but not on the fungus or the dead attine workers.

Materials and methods

Collection of *G. hartmani* colonies

Two *G. hartmani* colonies were found when collecting colonies of *Trachymyrmex cornetzi* sp. 1 (hereafter *T. cornetzi*) and *Sericomyrmex amabilis* along road edges in Gamboa, Panama. Voucher specimens of all three species were deposited at the Zoological Museum in Copenhagen. The first *G. hartmani* colony (Gh1) was found on 13 March 2002, in the fungus garden of 1 of 71 (1.4%) collected colonies of *T. cornetzi*. Gh1 consisted of one dealate queen, around 500 workers, and many worker larvae and worker

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pupae. Neither the *T. cornetzi* ants nor their brood were present in the fungus garden. A *T. cornetzi* queen and 18 workers, but without fungus or brood, were clustered in an adjacent cavity 5 cm from the fungus garden.

The second *G. hartmani* colony (Gh2) was spread over 2 (12.5%) of 16 *S. amabilis* nests excavated in 2002. Gh2 was found late at night on 9 April 2002, in the process of migrating between these two *S. amabilis* nests. Several hundred *G. hartmani* workers emerged from nest Sa1, carrying larvae and adult males, but no pupae. *G. hartmani* walked in single file along an approximately 10 m long presumed odor trail and disappeared down the entrance of nest Sa2. The *G. hartmani* worker traffic was in both directions, but items were carried from Sa1 to Sa2 only. We observed the migration between 23:00 and 0:30 hours, by which time the traffic intensity had decreased slightly. No live *S. amabilis* were seen, but hundreds of dead *S. amabilis* workers were piled around the entrance of Sa2. Both Sa1 and Sa2 were excavated the next morning. One chamber in Sa1 was partly filled with a healthy fungus garden, in which a live *S. amabilis* queen and 40 *S. amabilis* workers without brood were found. Fifteen additional chambers were devoid of fungus but were occupied by about 150 *G. hartmani* workers and 272 *G. hartmani* males. Sa2 consisted of 11 chambers, all filled with healthy fungus gardens. Approximately 600 *G. hartmani* workers, 78 *G. hartmani* males, and many *G. hartmani* larvae were spread throughout the fungus gardens. *S. amabilis* callow workers, pupae, and larvae were also present in the fungus gardens, but no mature workers. We did not find a *G. hartmani* queen in either Sa1 or Sa2. We assumed that the *G. hartmani* in Sa1 and Sa2 were members of the same colony and that the migration had not yet been completed during the night. No aggression was observed after the *G. hartmani* from both nests were joined into a single colony Gh2.

Scouting behavior of *G. hartmani*

On five occasions in March–June 2002, solitary *G. hartmani* workers were observed walking during the day around nest aggregations of *Trachymyrmex* and *Sericomyrmex*. They showed a striking searching behavior, briefly entering every natural cavity or small hole in their path. This behavior strongly suggested that these workers were scouting for new colonies for usurpation.

Colony raiding

Colonies Gh1 and Gh2 were set up in the laboratory for behavioral observations and video recording. Unfortunately, the dealate queen from Gh1 died during transport from the field to the laboratory. Each colony was set up in two 8×6×5 cm plastic boxes joined with a tube. We placed moist cotton wool in each nest box to maintain humidity. Between March and May 2002 we staged a total of six artificial raids by *G. hartmani* on queenless *T. cornetzi* ($n=4$) and *S. amabilis* ($n=2$) colonies. The *T. cornetzi* and *S. amabilis* colonies were kept in nest boxes as described above. Colony raids were provoked by connecting the *G. hartmani* nests to the attine nests with a 5 cm long tube.

Results

The outcomes of the raids were similar and did not differ between the two host species. The first *G. hartmani* workers entered the attine nest within minutes after joining the nests. This incited the attines to run around agitatedly. The *G. hartmani* occasionally attacked attine workers, stinging them to death. The attine workers did not attack the *G. hartmani* but ran away from them, without coming into physical contact. The stereotypical



Fig. 1 Top to bottom *G. hartmani* worker, dealate queen, and male

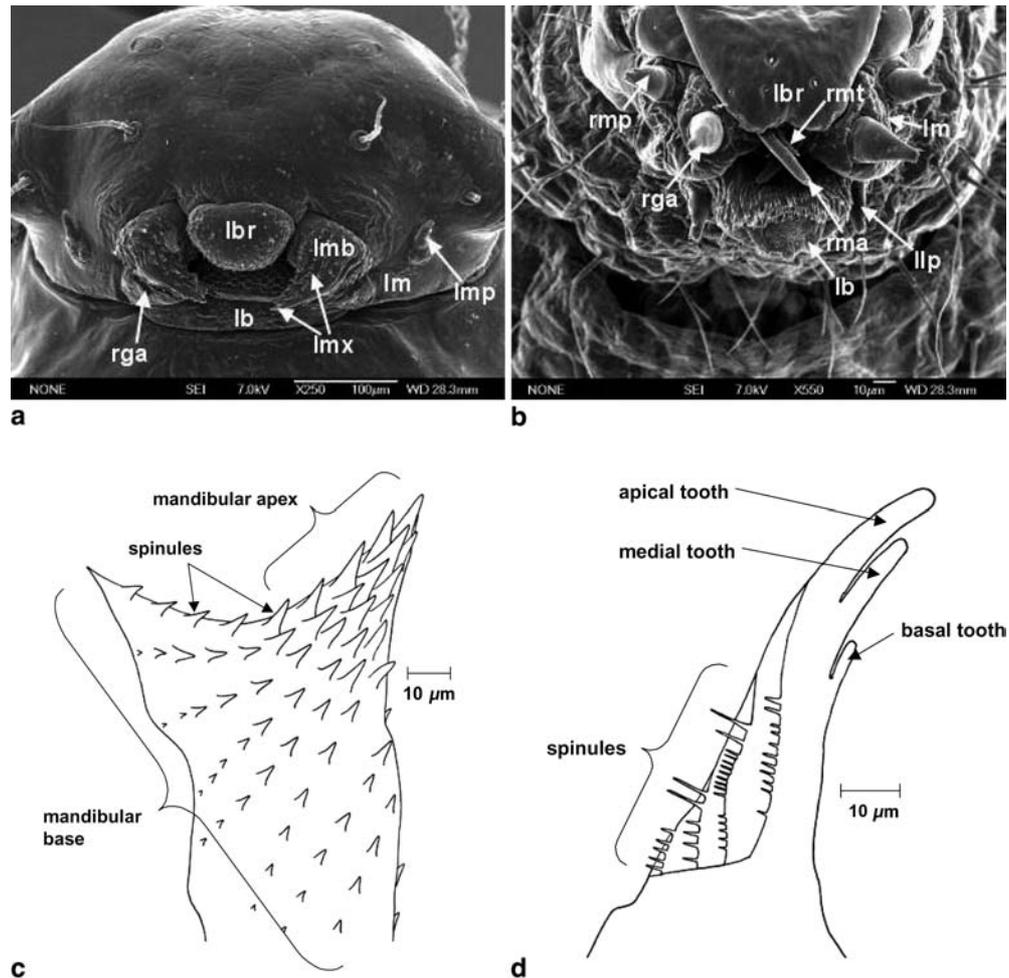
reaction of *S. amabilis* to human disturbance of the nest, curling up and remaining motionless, was not observed during the artificial raids. We observed two types of presumed recruiting behavior by *G. hartmani*: (1) workers marked the connection tube with the tip of the gaster; and (2) workers returned into the *G. hartmani* nest box and ran around in an irregular pattern among their nest mates. These behaviors resulted in large numbers of *G. hartmani* workers moving to the attine nest. The attine workers collected larvae, pupae, and bits of fungus from the fungus garden and absconded toward the far corner of the nest box where they were left undisturbed by the *G. hartmani*. The attine workers all died within a few days, possibly from dehydration. The entire nest takeover took only 2–5 min. The *G. hartmani* moved their brood into the center of the fungus 1–6 days after the nest takeover. In one experiment, the *T. cornetzi* established a small fungus garden on the ceiling of the nest box, which died after 2 days.

Exploitation of usurped fungus gardens

G. hartmani workers and larvae fed on the usurped fungus gardens of *T. cornetzi* and *S. amabilis*. Workers cropped

Fig. 2 **a** SEM image of the mouthparts of a *Trachymyrmex cornetzi* sp. 1 second instar worker larva. Note the spinules covering the entire surface of the mandibles. **b** SEM image of the mouthparts of a *Gnamptogenys hartmani* second instar worker larva. The mandibular spinules are hidden from view by the labrum and the maxillae. *lb* labium; *lbr* labrum; *llp* left labial palp; *lm* left maxilla; *lmb* left mandibular base; *lmp* left maxillary palp; *lmx* left mandibular apex; *rga* right maxillary galea; *rma* right mandibular apical tooth; *rmp* right maxillary palp; *rmt* right mandibular medial tooth.

c Diagram of the right mandible of a *T. cornetzi* sp. 1 final instar worker larva, dissected loose and viewed dorsally under a light microscope. **d** Diagram of the left mandible of a *G. hartmani* second instar worker larva, dissected loose and viewed dorsally under a light microscope



fungus from the garden surface, masticated and ingested it in a similar manner to attine and *Megalomyrmex* ants (Adams et al. 2000). Like most ponerine larvae, *G. hartmani* larvae are of the pogonomyrmecoid type (Wheeler and Wheeler 1976). *G. hartmani* larvae used their flexible thoracic neck, typical of pogonomyrmecoid larvae, to graze on the fungus surface. Workers also masticated the attine brood, ingested it or fed it to their larvae. They did not eat dead attine workers but did cut up and eat their dead *G. hartmani* nest-mates. *G. hartmani* workers were never observed to add to or modify the fungus gardens. They ignored dried flower petals, which are readily used by captive colonies of *T. cornetzi* and *S. amabilis* as fungus substrate. Their fungus harvesting was inefficient: large proportions of fungus were not eaten but were moved to the side by the *G. hartmani* as it deteriorated. The fungus gardens were completely dead after 4–13 days.

G. hartmani larval mouthparts

We compared the mouth parts of larvae of *G. hartmani* with light- and scanning-electron microscopy (SEM) to

determine whether *G. hartmani* and attine larvae showed any convergent adaptations to their fungal diet, using *T. cornetzi* for comparison. *T. cornetzi* larval mandibles (Fig. 2a, c) are of the attoid type typical of attines, which is thought to be specifically adapted for masticating fungus (Wheeler and Wheeler 1976; Schultz and Meier 1995). *T. cornetzi* larval mandibles are shaped like fleshy, rounded cones and are entirely covered with robust spinules, 1–11 μm long and 1–3.5 μm wide (Fig. 2d). In contrast, *G. hartmani* larval mandibles (Fig. 2b, d) are of the ectatommoid type (Wheeler and Wheeler 1976), partly overlapping, and ending in three mandibular teeth that are seemingly suited for cutting insect prey. The mandibles bear four parallel rows of slender spinules, 1.5–7 μm long and 0.5–1 μm wide (Fig. 2d), along the exterior margin. In all aspects, *G. hartmani* larval mandibles are similar to those described for *Gnamptogenys* species with a non-fungal diet (Wheeler and Wheeler 1976). Wheeler and Wheeler (1976) singled out the attines and the genus *Gnamptogenys* as the two ant taxa in which larval mandibular spinules are most strongly developed. The function of the spinules in *Gnamptogenys* is unknown, but the spinules are thought to puncture the chitinous cell walls of fungal hyphae and

gongylidia in attines (Wheeler and Wheeler 1976). In *G. hartmani*, the spinules may have a comparable function, holding and puncturing bits of fungus that are held between the mandibles and the labrum. Thus, there is no evidence that *G. hartmani* larvae evolved new adaptations to a fungal diet. However, the presence of long spinules on the larval mandibles in the genus *Gnamptogenys* may have pre-adapted *G. hartmani* to fungus eating.

Discussion

G. hartmani displays marked adaptations to an agro-predatory lifestyle. First, workers can locate attine ant nests and recruit nest-mates to them. Second, the striking “panic” reaction by attine workers when confronted by only a few *G. hartmani* workers suggests that *G. hartmani* uses propaganda substances (Lenoir et al. 2001) to facilitate nest usurpation. Third, whole colonies can migrate in a coordinated manner to a new nest when they have exhausted the fungus and brood. Fourth, the workers are tolerant toward the absconded attine ants, allowing them to grow a new fungus garden that could be raided in the future. Fifth, like *Megalomyrmex* sp. nov., *G. hartmani* workers and larvae feed on the host brood and fungus garden. In contrast to *Megalomyrmex* sp. nov., which reshapes the fungus garden but does not add substrate to it (Adams et al. 2000), *G. hartmani* appears unable to maintain the fungus gardens in any way. However, the low survival rates of fungus gardens in our usurped laboratory colonies may be partly artifactual. This is because no callow workers were present in the queenless attine colonies that we offered for usurpation, while our field observations show that *G. hartmani* does not expel callow host workers from the fungus garden. However, the lack of active tending behavior may imply that *G. hartmani* needs to migrate more frequently than *Megalomyrmex* sp. nov. The time between migrations may also depend on the colony size of *G. hartmani* and its host species. Presumably, a *T. cornetzi* nest with its single fungus garden will be depleted more quickly than an *S. amabilis* colony with many fungus gardens, and large *G. hartmani* colonies will exhaust the resources in usurped nests more quickly than small *G. hartmani* colonies.

Several other *Trachymyrmex* and *Sericomyrmex* species occur in the same locality as *S. amabilis* and *T. cornetzi* and may serve as additional hosts. *G. hartmani* is maybe less likely to usurp colonies of the more basal attine genera, such as *Myrmicocrypta*, *Mycocepurus*, or *Cyphomyrmex*, because of the small sizes of their fungus gardens, which probably could not sustain the large number of workers in a *G. hartmani* colony. At the other end of the colony size spectrum, mature colonies of *Atta* and *Acromyrmex* leafcutter ants are probably too large to be usurped by *G. hartmani*, although young leafcutter ant colonies might be usurped successfully.

The method of colony founding in *G. hartmani* is unknown. Usurping an attine colony will be difficult for a

single founding *G. hartmani* queen. A life history based on colony fission or budding seems therefore likely. *G. hartmani* queens are smaller than males (Fig. 1) and the sex ratio in the two excavated colonies was highly male biased. This may indicate an “army ant mode” of colony founding through fission, with males dispersing between colonies and queens mating in the nest.

The behavioral ecology of *G. hartmani* appears unique within its genus. Many *Gnamptogenys* species are generalist predators, or specialize on beetles or millipedes (Lattke 1995). However, at least one other species is known to be a predator of ants, while the feeding habits of many species are poorly known (Lattke 1995). Our observations show that *G. hartmani* is partly nocturnal. If this applies to other *Gnamptogenys* as well, it may help explain the current lack of behavioral ecology data for many *Gnamptogenys* species.

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