## Research article

# Nesting biology of the arboreal fungus-growing ant *Cyphomyrmex cornutus* and behavioral interactions with the social-parasitic ant *Megalomyrmex mondabora*

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Received 14 September 2006; revised 1 February 2007; accepted 6 February 2007.

**Abstract.** We describe the extraordinary nesting habits of the fungus-growing ant Cyphomyrmex cornutus (Formicidae, Myrmicinae, Attini) and the natural history of Megalomyrmex mondabora (Formicidae, Myrmicinae, Solenopsidini), a social parasite that inhabits nests of C. cornutus and other small attine ants. The study was carried out at two sites on the Atlantic slope of Costa Rica. The C. cornutus nest is an oblong mass of accreted soil, attached to or suspended from low vegetation in wet forest understory. Less than a fourth of the nest volume has chambers and is inhabited by C. cornutus; the remainder is a semi-solid mass of accreted soil often housing a variety of arthropods, including other unspecialized commensal ant species. Five C. cornutus colonies examined were parasitized by M. mondabora. Colonies of M. mondabora inhabited chambers very near those of the host. In laboratory observations, M. mondabora and C. cornutus workers interacted with little aggression despite the consumption of C. cornutus larvae and fungi by M. mondabora. During most interactions, C. cornutus workers responded submissively, whereas M. mondabora appeared indifferent or nonresponsive. Megalomyrmex mondabora parasitizes several other attine species (Cyphomyrmex costatus, Cyphomyrmex salvini, and Apterostigma goniodes), and it appears therefore a relatively unspecialized social parasite with broad attine hostassociation. The size of M. mondabora workers vary with host species, suggesting M. mondabora sensu lato comprises either cryptic species or the host environment affects worker size.

Keywords: Cyphomyrmex cornutus, Megalomyrmex mondabora, social parasitism, nesting biology.

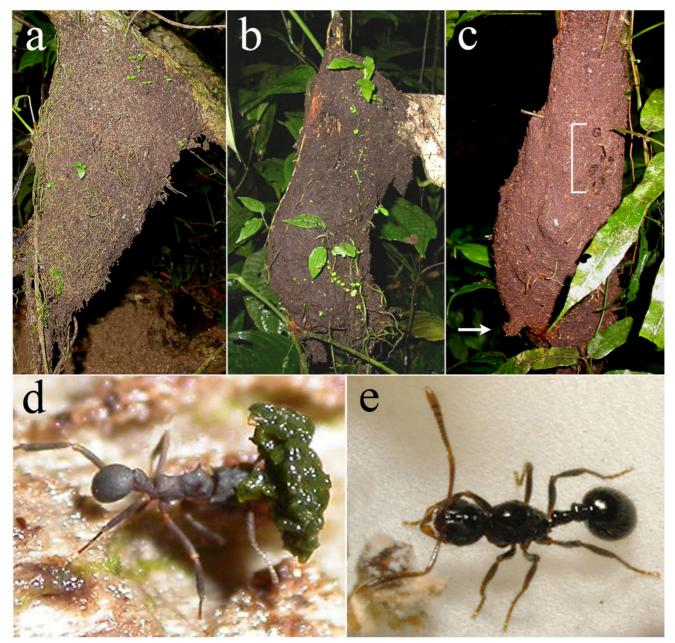
#### Introduction

The ant tribe Attini comprises the so-called fungusgrowing ants, a group receiving increased attention as a model of coevolution and mutualism (Mueller, 2002; Currie et al., 2003; Mueller et al., 2005). The biology of the Attini involves not only their mutualistic association with a variety of fungal symbionts, but also a host of specialized predators and pathogens (Mueller, 2002; Currie et al., 2003). Among these are social parasites defined as one social organism parasitizing another social organism, in the ant genus Megalomyrmex (Brandão, 1990; Adams et al., 2000a; Mueller et al., 2001). Heretofore the relationship between attine ants and Megalomyrmex has been difficult to study because the associations generally occur underground in small and cryptic attine nests. We describe here the unique arboreal nests of the attine ant Cyphomyrmex cornutus (Figs 1a,b,c) and the occurrence of the social parasite Megalomyrmex mondabora in those nests.

The genus *Cyphomyrmex* is one of the most abundant and species-rich genera in the tribe Attini (Bolton, 1995). Most *Cyphomyrmex* species are diminutive ants that nest in soil or leaf litter. Colonies are small, with tens to hundreds of workers. Workers in most species harvest insect feces (Fig. 1d) and diverse vegetable debris (e.g., decaying flower parts) as substrate for their yeast garden. *Cyphomyrmex cornutus* is a highly distinctive species that occurs from Costa Rica to Ecuador (Kempf, 1968, Snelling and Longino, 1992). The only natural history information accompanying the species description is that the type specimens were found within rocky wet ravines ("quebrada") and in lowland rainforest (Kempf, 1968). Snelling and Longino (1992) reported additional locality

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**Figure 1.** The three main nest types of *Cyphomyrmex cornutus* ants: (a) beard-shaped, (b) pendant or free-hanging (nest suspended from small vine at the top and the side under dead leaf), (c) attached (nest was attached to the side of a small tree). Multiple entrances from the *C. cornutus* nest can be seen at the top (next to the bracket). The large turret at the bottom of the nest (see arrow) is the *M. mondabora* entrance. (d) *C. cornutus* forager carrying insect frass (e) *M. mondabora* queen.

records but no new natural history information. Our field observations of *C. cornutus* reveal that it has a highly distinctive nesting biology that is unlike any other *Cyphomyrmex* species. The nests are large masses of accreted soil suspended in the low arboreal zone (Figs 1a,b,c). Colonies are large, with a thousand or more workers, and the nest structure houses not only the *Cyphomyrmex* colony but also many other cohabiting ant species as well as other arthropods, including the social parasite *M. mondabora* (Figs. 1c,e).

Social parasitism has evolved multiple times in ants and other social hymenopterans (Buschinger, 1986; Hölldobler and Wilson, 1990; Carpenter et al., 1993; Cervo and Dani, 1996; Pedersen, 1996). Although in many cases they remain rare relative to the abundance of the host, social parasites can severely affect host colony fitness by exploiting key behaviors related to parental care or by consuming brood and/or food stores (Hölldobler and Wilson, 1990). The Attini suffer from social parasites and agro-predators (species that usurp the

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fungus garden from the attine ants) in the genera Pseudoatta, Acromyrmex, Gnamptogenys, and Megalomyrmex (Brandão, 1990, 2003; Adams et al., 2000a; Bekkevold and Boomsma, 2000; Dijkstra and Boomsma, 2003; Boomsma, 2004). The first two are social parasites derived from ancestral fungus-growing ant lineages within the Attini, whereas both Gnamptogenys and Megalomyrmex originated independently in lineages distantly related to their attine hosts. The two *Pseudoatta* species are considered advanced social parasites in that they no longer have a worker cast and do not resemble their host (Hölldobler and Wilson, 1990; Delabie et al., 1993; Schultz et al., 1998). Acromyrmex insinuator is a less advanced social parasite that resembles its congeneric host and still retains a minimal worker cast. It is considered a transitional or incipient social parasite that is in the process of evolving more derived features (Schultz et al., 1998; Sumner et al., 2004).

Megalomyrmex is distantly related to Attini and belongs to the Solenopsidini, containing thief ants and fire ants (Bolton, 2003). The genus is made up of both free-living and social-parasitic species found in wet and subtropical forests from southern Mexico to Argentina (Brandão, 1990; 2003). The 31 known species have been divided taxonomically and behaviorally into the *leoninus*, pusillus, modestus, and silvestrii species groups (Brandão, 1990). Most species are unassociated with the fungusgrowing ants and are free-living (non-parasitic). Eight species, classified in the *silvestrii* group, are assumed to be associated with fungus-growing ants (Brandão, 1990). These associations may be facultative or obligate and may involve host brood predation and fungal (agro-) predation (Adams et al., 2000a; Brandão 1990; 2003; RMMA pers. obs.). Megalomyrmex wettereri, an obligate agropredator, aggressively attacks attine host ants and usurps their gardens and nest cavities (Adams et al., 2000a). Megalomyrmex symmetochus lives peacefully with its attine hosts and is an obligate social parasite (Wheeler, 1925). We report here that M. mondabora also appears to be an obligate social parasite living peacefully with its attine hosts, consuming host larvae and fungus-garden.

# **Materials and methods**

John Longino (JTL) observed 11 separate colonies of *C. cormutus* during multiple collecting trips to Costa Rica between 1985 and 2003. The nests were found on the Atlantic slopes of the Cordillera de Guanacaste, Cordillera de Tilarán, Cordillera Volcánica Central, and Cordillera de Talamanca. Two of these nests contained *M. mondabora*. Rachelle Adams (RMMA) carried out a survey of *C. cormutus* nests during February and August 2003 and June 2005 at two localities in Costa Rica. Both sites were on the Atlantic slope of Volcan Barva in the Cordillera Volcánica Central. One site was the Cascante Refuge (11 km SE La Virgen, 450–550 m, 10°20'N, 84°04'W), on the Barva transect in Braulio Carrillo National Park (Pringle et al., 1984; Hartshorn and Peralta, 1988). The other site was La Selva Biological Station (10°26'N, 84°00'W, 50 m), 15 km down slope from the Cascante Refuge (McDade et al., 1993). Both sites are tropical wet forest.

RMMA examined a total of 75 C. cornutus nests, 35 from Cascante (Feb. 2003) and 40 from La Selva (Aug. 2003). At La Selva, nests were found on the side of the trail and meters were paced off from meter markers to indicate location, shape was recorded, and physical dimensions were measured. All nests at both sites were examined for the presence of M. mondabora and nests at La Selva were examined for other ant species on the surface. Nests were inspected in the field by first observing activity on the surface, searching entrances, and then carefully removing one side of the nest structure, which was removed by carefully scraping off layers with featherweight forceps. The nest material was sufficiently rigid to allow the creation of a window into the nest chambers without nest collapse. Most of the solid soil mass at the bottom of the nest structure was left intact. In all but one case, the C. cornutus nests withstood the disturbance to their nest structure and repaired the damage within 24 hours. One colony moved their nest to a nearby site following examination.

The 40 *C. cornutus* nests that were marked at La Selva in 2003 were reexamined in 2005 and classified as live, uninhabited, moved, or not found. Nest structures that were empty, dry, and crumbling were considered uninhabited. A few colonies were suspected of moving nearby because there was an active nest within 25 cm of the old abandoned nest structure and containing a sizable colony. In a few cases flags for marking nests could not be found or were found with no remnants of the preexisting nest. These colonies either moved or were dead.

During the February 2003 survey, five nests were collected in their entirety. The five nests have collection reference numbers RMMA030213-09, AGH030212-13, RMMA030213-10, RMMA030212-07, and RMMA030213-07 but are referred to as nests one to five, respectively, in this paper. Nests #1, #2, and #5 contained a *M. mondabora* colony. Nests #3 and #4 were unparasitized. Only Nests #1–3 were thoroughly dissected and all contents counted. All three nests contained additional ant species known to be arboreal ants with generalized nesting habits, facultatively present in or on the *C. cornutus* nests.

Five subcolonies were established in 100 x 15 mm Petri dishes, using nesting material and 15–20 live workers per species from the collected nests. Four subcolonies contained yeast garden, *C. cornutus* workers and brood, and *M. mondabora* workers and brood. Subcolony A1 was from Nest #5, subcolonies B1, B2, and B3 from Nest #1. Subcolony C1 initially contained yeast garden, 15–20 *C. cornutus* workers and brood from Nest #4 (an unparasitized nest). The *C. cornutus* workers were allowed approximately four hours to acclimate to the Petri dish, then four workers of *M. mondabora* from Nest #1 were introduced. Brief behavioral observations were made sporadically over four days.

In 2005, two additional colonies from the Cascante site (RMMA050627-01 and RMMA050625-01, hereafter referred to as Nests #6 and #7) were studied using video recordings one to four days after their collection. Cyphomyrmex cornutus nests were laid on their side and placed in clear nestboxes (10 x 10 x 20.5 cm) with  $\frac{1}{2}$  cm of moistened plaster on the nestbox floor. The sides were painted with fluon to prevent the ants from escaping during observations. When ants were not observed, the nestbox was covered with a lid to retain moisture. Large roots, plants, and a portion of the soil were removed such that a flat layer of nesting substrate remained in the nest box. A large Petri dish (100 x 15 mm) covered in red cellophane was provided as a refuge for either species. Megalomyrmex ants were observed by following them with the camera or keeping the camera stationary above the colony. Thirty-seven minutes and 24 seconds of Nest #6 and 33 minutes of Nest #7 were examined, and 137 interactions were analyzed using slow and real time playback.

JTL, RMMA, and others made additional collections and qualitative observations on *M. mondabora* at multiple sites in Costa Rica and Panama. Worker size variation in *M. mondabora* was examined with respect to attine host.

### Results

#### Nest structure

Nests of *C. cornutus* are constructed of accreted soil. There are three main types of nest structures: beardshaped, pendant or free-hanging, and attached (Figs 1a,b,c). "Beard-shaped" nests hang vertically under a large branch, from near-horizontal surfaces (Fig. 1a). "Pendant" nests hang by small vines (some less than a centimeter in diameter) (Fig. 1b). "Attached" nests are broadly attached to a near-vertical surface, such as the base of an epiphytic plant or flat against a tree trunk or rock (Fig. 1c). Nests are usually penetrated with plant roots from nearby vines and epiphytes. The ants sometimes incorporate live or dead leaves into the nest and place insect feces on the surface. The top portion of the nest (approximately the upper fourth) has multiple nest entrances (Fig. 1c) and is filled with thin walled chambers built around roots, both speckled with the fungal garden. Large piles of beetle elytra, other insect fragments, and insect feces are incorporated into the fungus garden or are in close proximity. The fungus is the yeast form typical of Cyphomyrmex species in the rimosus-group, comprised of small polygonal masses that dot the surface of the substrate. The bottom portion of the nest is typically dense, with few passageways, and it is not inhabited by C. cornutus. There are often plant seedlings and/or mushrooms on the nest surface. These nests are not considered true "ant gardens" in the usual sense (Hölldobler and Wilson, 1990), because the plants never grow very large and they are not consistently present.

Cyphomyrmex cornutus colonies occur in both mature and secondary forest and are patchily distributed. They are often in very shaded and humid areas near ground level although the canopy was not surveyed in this study. At La Selva, C. cornutus is very abundant in second growth on the STR trail and rare or absent on most other trails. The average height of nests from the ground (measured from the base of the nest) was 120.2 cm (n=37; range 71.1-205.7 cm). The average length of the nest was 20.1 cm (n=35; range 8.8-40.6 cm), and the average width was 10.1 cm (n=34; range 5.08-15.24 cm). The average circumference, measured only for the pendant and beard-shaped nests, was 26.8 cm (n=14; range 12.7-38.1 cm) and the depth, only measured on a few "attached" nests, averaged 4.6 cm (n=8; range 2.5-6.4 cm). Eleven nests observed by JTL at various localities showed qualitatively similar patterns of nest size, location, and shape, although one nest was imbedded in a cavity in the trunk of a large Xanthosoma sp. (Araceae). In all cases the length of the nest exceeded the width, resulting in a vertical, oblong shape. Whole colony counts of C. cornutus revealed that worker populations could be in the thousands and colonies are monogynous (Table 1).

### Colony survival rate

In 2005, survival rates of the 40 colonies marked and measured in 2003 were determined. Of the 40 nests observed in 2003 nine remained alive (22.5%), 22 were inactive (55%), seven could not be found (17.5%), and two colonies appeared to have moved to new nests close by (5%).

## Commensal associates and guest ant colonies

Eighteen out of 40 (45%) nests examined at La Selva had additional ant species on their surface or subsurface (Table 2). A total of 10 species were collected, most of them single occurrences. However, Pheidole flavens was found on the surface or subsurface of 12 out of 40 nests (30%) at La Selva. One unidentified *Pheidole* queen and hundreds of Pheidole flavens workers were found in one dissected nest from Cascante (Table 1). A small colony of Pachycondyla bugabensis and colonies of a small unidentified Solenopsis were found in each of two Cyphomyrmex nests dissected by JTL. A nest dissected by Ulrich Mueller also contained a *Brachymyrmex* colony (Table 1, Nest #8). Qualitative examination of various dissected or subsampled nests revealed an abundance of additional arthropod life in the peripheral and lower portions of the nest, including annelids, beetle larvae, nematodes, isopods, and silverfish. It is unclear how close or codependent the associations are between C. cornutus and these "guests." It is likely that many or all of these species will also be found unassociated with C. cornutus, and they are perhaps opportunistic inhabitants, able to nest in various microhabitats similar to C. cornutus nests.

# Occurrence of M. mondabora in C. cornutus nests

Megalomyrmex mondabora occurred at low frequency in C. cornutus nests, and appeared to be more abundant at higher elevations. Two of the 11 (18.2%) C. cornutus nests examined by JTL contained M. mondabora colonies. RMMA's surveys revealed colonies of M. mondabora in three of 35 (8.6%) C. cornutus nests at Cascante in 2003 and two of five (40%) in 2005, and none in the 40 nests at La Selva. One of the three M. mondabora colonies collected at Cascante was first found by JTL in 2002, then was resurveyed by RMMA in 2003. It contained over 100 workers and many alate queens and males when discovered in June 2002, and in February 2003, the nest contained 249 workers and no alates (Table 1, Nest #1). The two whole colony counts of M. mondabora revealed single queens and worker populations of about 250. Although the M. mondabora colonies were found in chambers very close to C. cornutus nest chambers, they maintained a separate entrance and could be found on the nest surface or near the nest on the ground. The entrance varied in conspicuousness, from having a large turret shaped entrance (Fig. 1c) to having no entrance superstructure.

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**Table 1.** Colony counts, including commensals and social parasites of four *C. cornutus* colonies, two of which are parasitized by *M. mondabora*. Nests #1, #2, and #3 were collected in February 2003 at the Cascante Refuge on the Barva Transect, Braulio Carrillo National Park, Costa Rica. Nest #8, collection reference number UGM020604-07, was collected by U. Mueller in 2002, on Punta Pena Road, Panama (commensal ant workers were not counted).

Nest ID and association	Ant species	Workers	Dealate queens	Alate queens	Alate Males
Nest #1					0
Host	Cyphomyrmex cornutus	2657	1	0	0
Social parasite	Megalomyrmex mondabora	249	1	0	0
Commensal	Solenopsis JTL-005	4	3	0	0
Commensal	Strumigenys biolleyi	>20	0	0	0
Commensal	Pachycondyla cf. villosa	5	0	0	0
Nest #2					
Host	Cyphomyrmex cornutus	208	1	0	9
Social parasite	Megalomyrmex mondabora	260	1	0	12
Commensal	Odontomachus hastatus	0	1	0	0
Commensal	Pheidole sp.	0	1	0	0
Commensal	Pheidole flavens	>100	0	0	0
Nest #3					
Host	Cyphomyrmex cornutus	1105	1	10	0
Commensal	Crematogaster longispina	>20	0	0	0
Commensal	Hypoponera JTL-007	1	1	0	0
Commensal	Pachycondyla lineaticeps	9	2	0	0
Commensal	Paratrechina steinheili	18	0	0	0
Commensal	Pheidole JTL-052	8	0	0	0
Commensal	Solenopsis picea	1	0	0	0
Commensal	Strumigenys biolleyi	1	0	0	0
Nest #8					
Host	Cyphomyrmex cornutus	4117	0	190	138
Commensal	Brachymyrmex sp.	?	?	?	?

**Table 2.** Commensal ant species found associated with 18 out of 40 *C. comutus* colonies at La Selva Biological Station, Costa Rica. Commensal associates were collected from the surface and subsurface of *C. comutus* nest structures. Numbers indicate the number of nests on which each species was found. More than one commensal ant species may have been recorded on a given host nest.

Commensal ant species on nest surface	Number of <i>C. cornutus</i> nests (N=40)		
Apterostigma collare	1		
Brachymyrmex JTL-007	2		
Pheidole anastasii	1		
Pheidole flavens	12		
Pheidole perpusilla	1		
Pyramica alberti	1		
Solenopsis geminata	1		
Solenopsis picea	1		
Strumigenys micretes	1		
Wasmannia auropunctata	2		

# Laboratory observations of host-parasite interactions

On establishment of the four subcolonies (A1, B1, B2, and B3), the *C. cornutus* and *M. mondabora* workers immediately segregated in the Petri dishes. The *M. mondabora* workers often stole and consumed host brood and yeast garden. There was one instance of aggression observed by a *M. mondabora* worker towards a *C. cornutus* worker; when the *C. cornutus* worker approached the *M. mondabora* group, a *M. mondabora* worker quickly bit the head of the host worker. Otherwise interactions between the social parasites and the hosts appeared nonaggressive.

To investigate the initial interactions between host workers and an unfamiliar parasitic worker, *M. mondabora* workers were introduced to naïve *C. cornutus* workers from an unparasitized colony (C1) and the subcolony was continuously observed for 46 minutes following the introduction. Upon first contact, *C. cornutus* workers displayed aggression with open mandibles and a sudden jerking motion towards the *M. mondabora* 

workers. This aggressive display, described as "jumping" by Kweskin (2004), is also seen in related *Cyphomyrmex* species such as *C. costatus* (Kweskin, 2004), *C. muelleri* and *C. longiscapus* (RMMA pers. obs.). The *Megalomyrmex* workers responded to this aggression by touching the *C. cornutus* workers with their antennae. The *C. cornutus* workers then bowed their heads, tucked their antennae into their antennal scrobes, remained stationary for a few seconds, and then walked away. *Cyphomyrmex cornutus* workers reacted similarly following many interactions they had with the *M. mondabora* workers. Eventually the *M. mondabora* grouped separately from the host workers, as seen in the infected subcolonies described above.

In 2005, a more detailed analysis of host and parasite interactions was made for two additional parasitized C. cornutus colonies. As in 2003, both parasite and host colonies kept their brood, queen, and the majority of the workers isolated from one another. The C. cornutus workers maintained the separation by building a wall of soil and insect exoskeletons around the M. mondabora colony while Megalomyrmex workers helped shape it. Several M. mondabora ants wandered throughout the nestbox, often coming into contact with C. cornutus workers. One hundred thirty-seven interactions between M. mondabora and C. cornutus workers were analyzed. Contact was initiated by M. mondabora workers 47 times (34.3 %), by *C. cornutus* workers 66 times (48.2 %), and by both simultaneously 24 times (17.5%). The three responses of the host and/or parasite following an interaction were indifference (no response), submissive response, and "twitching." The submissive response, only seen in the host species, begins with a downward tilt of the head, antennal retraction into the scrobes, and a slight gaster tuck (in one case the observation was made from the side and the gaster was vibrating faintly). Twitching, also only seen in the host species, was a quick backward motion on the horizontal plane while the body curled further. This behavior was different than jumping which is a forward motion only seen during parasite introduction to a naïve host. Twitching variably occurred following the submissive response. In all cases the M. mondabora reacted with indifference. The C. cornutus on the other hand were either indifferent (n=104), exhibited a submissive posture followed by motionlessness (n=7), or exhibited a submissive posture, became motionlessness and then twitched (n=26). The duration of the submissive posture (including twitching) ranged from 1.67 s to 13.96 s (mean 4.82) and the number of twitches they exhibited ranged from 2 to 17 (mean 5.19).

# Host use and worker size variation in M. mondabora

Megalomyrmex mondabora occurs in Costa Rica, Panama, and Brazil (Brandão, 1990; RMMA, pers. obs.). The type specimens of *M. mondabora* were collected by W. L. Brown near Turrialba, Costa Rica. They were collected from the fungus nest of a small unidentified *Apterostigma* 

species (Brandão, 1990). JTL collected M. mondabora three times: (1) nocturnal foragers on dead wood at Refugio Eladio, a site at 800 m elevation on the Río Peñas Blancas on the Atlantic slope of the Cordillera de Tilarán (10°19'N 84°43'W); (2) a colony inside a nest of C. cornutus at Estación Pitilla, a site at 600 m elevation on the Atlantic slope of the Cordillera de Guanacaste  $(10^{\circ}59^{\circ}N 85^{\circ}26^{\circ}W)$ ; and (3) a colony inside a nest of C. cornutus at Refugio Cascante, one of the sites of RMMA's surveys. RMMA found a total of six M. mondabora colonies at the Cascantae site. In 2003, a single M. mondabora queen was collected in a Cyphomyrmex salvini nest and three other colonies containing workers were collected in C. cornutus nests. In 2005, two additional colonies were collected within C. cornutus nests. Megalomyrmex mondabora has also been found associated with Apterostigma goniodes and Cyphomyrmex costatus in Panama (RMMA, pers. obs.).

The workers from these collections are all very similar in gross morphology and the diagnostic features of the species. Intracolonial size variation is small, but there is high inter-colony size variation, and this variation is related to host. Six records of M. mondabora from C. cornutus have head length 0.87-0.96 mm, three records Apterostigma goniodes have head length 0.76-0.79 mm, and one record from C. costatus has head length 0.67. The size of the M. mondabora workers may parallel the amount of food available: C. cornutus workers are large and the fungus gardens are large, A. goniodes workers are about the same size as C. cornutus workers but the colony and fungus garden is smaller (although the latter is in a mycelium form and therefore may not be comparable to yeast gardens), and both workers and fungus gardens of C. costatus are smaller than those of A. goniodes.

## Discussion

Cyphomyrmex species are known to nest in the soil, in shallow cavities along stream embankments, under stones and logs, in the leaf litter, within subarboreal cavities, in rotting logs, and in dead wood suspended in vegetation, and under epiphytes. Many of these nest structures are partially or wholly constructed of accreted soil. Here we have described the nest structure of a species of Cyphomyrmex that not surprisingly shares some of these nesting characteristics. What makes C. cornutus unusual is their large nest and colony size. Many Cyphomyrmex colonies contain fewer than 100 to a few hundred individuals, whereas C. cornutus colonies may have over 1000 individuals. In addition, the large nest structures built by C. cornutus accommodate numerous additional ant and arthropod species, one being the social parasite M. mondabora.

Megalomyrmex mondabora colonies are specialist parasites of fungus-growing ants and they do not appear to nest independently, outside this association. Intensive Insect. Soc. Research article 7

collecting of the ant fauna at La Selva in Costa Rica (Longino et al., 2002) and elsewhere on the Barva Transect has never yielded a M. mondabora colony unassociated with an attine host. Mike Kaspari's numerous samples of leaf litter ants from 1 m<sup>2</sup> plots in Panama have also never yielded a free-living M. mondabora colony (M. Kaspari, pers. comm.). Megalomyrmex mondabora workers can be found on the outside surface of the host's nest during the day and out scouting or foraging at night. It is possible that workers forage outside their host colony in order to meet nutritional requirements. Megalomyrmex mondabora is the second species reported to eat host larvae, paralleling earlier reports on M. wettereri (Adams et al., 2000a,b). Fungal and larval consumption suggests a parasitic relationship between M. mondabora and C. cornutus, although true host fitness impact is still

The behavioral interactions reported here are not unique to *C. cornutus* but are found in other *Megalomyrmex* host species. When a *C. longiscapus* colony is usurped by *M. wettereri*, the *C. longiscapus* ants will tuck their heads, just as described for *C. cornutus*, and will often curl up and play dead when being attacked (Adams et al., 2000a,b). *Trachymyrmex* cf. *zeteki* also exhibits a submissive posture when *Megalomyrmex symmetochus* approaches (Tseng and Adams, 2006). The cause of this dramatic reaction seen across host genera is unknown. Like other Solenopsidini genera, *Megalomyrmex* produce venom alkaloids (Jones et al., 1982, 1991). These and other behavioral cues might induce the submissive responses.

### Host related worker size variation

Megalomyrmex mondabora populations, occupying different host species, do not vary greatly in morphology with the exception of size. This variation may be caused by environmental or genetic mechanisms, or both. The host nest environment may influence development of Megalomyrmex larvae, through quality or quantity of food. Alternatively, M. mondabora sensu lato may be comprised of cryptic species or races, such that genetically distinct populations or species are specialized on particular attine host species.

The Megalomyrmex-Attine system is ideal for examining if populations specializing on a multiple host species are diverging and becoming genetically isolated, eventually leading to speciation. This hypothesis could be tested in several Megalomyrmex species (M. mondabora, M. symmetochus, M. silvestrii, and M. wettereri). M. mondabora parasitizes two yeast and two mycelium growing attine species in two genera (C. cornutus, C. salvini, C. costatus, and Apterostigma goniodes). Megalomyrmex symmetochus parasitize at least three species (Trachymyrmex cf. zeteki, Sericomyrmex amabilis, and a smaller Sericomyrmex species) (Wheeler, 1925; Brandão, 2003) and M. silvestrii parasitizes four species from four

genera (*Apterostigma* sp. 1, *C. costatus*, *Sericomyrmex* sp. 1 and *Trachymyrmex* sp. 1) (Weber, 1941; Kempf and Brown, 1968; Brandão, 2000; RMMA, pers. obs.). Finally, *M. wettereri* parasitize *Trachymyrmex bugnioni* and are agro-predators of *Cyphomyrmex longiscapus*, usurping the garden rather than cohabiting with the host (Adams et al., 2000a; Brandão, 2003). It would be interesting to know if *Megalomyrmex* species associating with multiple host species show size variation and/or are genetically isolated.

Our studies reveal a *Cyphomyrmex* species and a socially parasitic *Megalomyrmex* species with remarkable natural history, ideally suited for the study of social parasitism. Once a population is located, *C. cornutus* foragers can be baited with ground corn or rice and nests can be easily found and monitored. Most nests are within reaching distance (120.2 cm from the ground) and some can be collected by simply clipping the vines from which they are hung. Although fast moving for attine ants, the majority of the workers can be captured by this method. In addition, commensal and parasitic ant colonies can also be collected in their entirety, facilitating the study of the symbiotic community of these species.

## Acknowledgments

The work was supported by National Science Foundation grant DEB-0072702 (Project ALAS), a Dorothea Bennett Memorial Graduate Fellowship and a Hartman Fellowship, both from the University of Texas at Austin. We thank Ulrich Mueller, Anna Himler, and Natalia Biani for initial comments on the manuscript and Nicole Gerardo and the second anonymous reviewer for final comments. Some collections and laboratory assistance were generously provided by Anna Himler (AGH), Ulrich Mueller (UGM), Hermogenes Fernandez-Marín, Cameron Currie, Lisa Schonberg, Chris Roesel, Lauren Lacey, and Ximena Bernal. The photograph in Figure 1e was taken by Gregory Dimijian. Collections at the Cascante site were in conjunction with a Project ALAS expedition. Vouchers are deposited at the U. S. National Museum of Natural History; the Instituto Nacional de Biodiversidad, Costa Rica; and the collection of J.T. Longino at The Evergreen State College.

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