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Acromyrmex ameliae sp. n. (Hymenoptera: Formicidae): A new social parasite of leaf-cutting ants in Brazil

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Abstract The fungus-growing ants (Tribe Attini) are a New World group of > 200 species, all obligate symbionts with a fungus they use for food. Four attine taxa are known to be social parasites of other attines. *Acromyrmex* (*Pseudoatta*) *argentina argentina* and *Acromyrmex* (*Pseudoatta*) *argentina platensis* (parasites of *Acromyrmex lundi*), and *Acromyrmex* sp. (a parasite of *Acromyrmex rugosus*) produce no worker caste. In contrast, the recently discovered *Acromyrmex insinuator* (a parasite of *Acromyrmex echinatior*) does produce workers. Here, we describe a new species, *Acromyrmex ameliae*, a social parasite of *Acromyrmex subterraneus subterraneus* and *Acromyrmex subterraneus brunneus* in Minas Gerais, Brasil. Like *A. insinuator*, it produces workers and appears to be closely related to its hosts. Similar social parasites may be fairly common in the fungus-growing ants, but overlooked due to the close resemblance between parasite and host workers.

Key words *Acromyrmex*, leaf-cutting ants, social evolution, social parasitism
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Introduction

The fungus-growing ants (Tribe Attini) are a New World group of > 200 species, all obligate symbionts with a fungus they use for food. The Attini are found across the American continents and the West Indies and comprise at present > 200 described species in 13 genera. Two genera, *Atta* and *Acromyrmex*, are called leaf-cutting ants because most species culture their fungus on freshly cut foliage and flowers (Müeller *et al*., 2001). This particular foraging behavior makes these ants major agricultural pests.

Social parasitism, the exploitation of the nest of another species without contributing to colony maintenance, for example the cultivation of a fungus garden, has been reported occasionally in the attine ants. *Megalomyrmex* species can coexist as social parasites in attine colonies, consuming the fungus garden (Brandão, 1990; Adams *et al*., 2000). *Gnamptogenys hartmani* is also a specialized agro-predator of *Trachymyrmex* and *Sericomyrmex* fungus-growing ants in Panama (Dijkstra & Boomsma, 2003). Four *Acromyrmex* taxa are known to be social parasites of other *Acromyrmex* species, living in and feeding on their fungus gardens, but not contributing to its maintenance: *Acromyrmex* (*Pseudoatta) argentina argentina* and *Acromyrmex* (*Pseudoatta) argentina platensis* (parasites of *Acromyrmex lundi*), and *Acromyrex (Pseudoatta)* sp. (a parasite of *Acromyrmex rugosus*) produce no worker caste (Santschi, 1926; Bruch, 1928; Gallardo, 1929; Delabie *et al*., 1993). In contrast, the recently discovered *Acromyrmex insinuator* (a parasite of *Acromyrmex echinatior*) does produce workers (Schultz *et al*., 1998). Sumner *et al*. (2004) found that *Acromyrmex* (*Pseudoatta*) sp. was not closely related to its host, but *A. insinuator* was closely related to its host, *A. echinatior*. Here, we describe a new species, *Acromyrmex ameliae*, a social parasite of *Acromyrmex subterraneus subterraneus*

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and *Acromyrmex subterraneus brunneus* in Minas Gerais, Brasil. Like *A. insinuator*, it produces workers and appears to be closely related to its hosts.

Material and methods

In October 6, 2003, we excavated two colonies of the leaf-cutting ant *Acromyrmex subterraneus brunneus* Forel in Paraopeba, Minas Gerais State (MG), Brazil (19° 17'S; 44° 29'W). In one of these nests, we found one smaller queen together with the host queen. The other nest contained several male and queen alates later identified as parasite species, and these coexisted with the host queen. Both nests had an abundant number of workers. In another field expedition, in the same area, on April 20, 2004, we collected four additional nests of *A. subterraneus brunneus* and eight of *A. subterraneus subterraneus*, all of them parasitized by the same social parasite. Approximately 70% of the nests were parasited in the study area, a eucalyptus stand. The separation of males and queens of the parasite and host was easy, since the former were much smaller than the latter. Specimens of the studied material were deposited at the Myrmecology Laboratory in CEPLAC, Bahia State; at the Zoology Museum of University of São Paulo (MZUSP) and at the Regional Museum of Entomology in Viçosa, MG, Brazil.

Specimens examined

The *Acromyrmex* genus is in need of a complete revision. Particularly, there are several names associated with *subterraneus*, the host species. Since the parasitism seems widespread in this genus it is possible that one of the early papers on taxonomy has already named this particular species. Thus, specimens of the five current host subspecies associated with *subterraneus*, according to Gonçalves (1961), were consulted. *Acromyrmex subterraneus subterraneus* (Forel, 1893), *A. subterraneus brunneus* (Forel, 1912), both collected in Paraopeba, MG, Brazil; *A. subterraneus molestans* (Santschi, 1925) from Viçosa, MG, Brazil; and *A. subterraneus peruvianus* (Borgmeier, 1940), types from Cartavio, Peru, deposed in the collection of MZUSP, São Paulo, Brazil. The comparison with *A. subterraneus ogloblini* (Santschi, 1933) was based only on the original description. All original descriptions and revisions of the involved species also were consulted for comparisons (Forel, 1901, 1912; Santschi, 1925, 1933, 1937; Borgmeier, 1940; Gonçalves, 1961; Schultz *et al.*, 1998). We employed the same procedure to distinguish the new species from *A. insinuator*, the attini parasite from *A. echinatior*.

Measurements

The following measurements were taken under a stereoscopic microscope (Leica DC300):

HL – Head length: maximum length of the cephalic capsule measured from the anterior margin of the clypeus to the midpoint of a line drawn across the posterior cephalic margin;

HW – Head width: maximum width of the head, excluding the eyes;

ML – Mandible length: straight-line length of a mandible (always the right), measured from the base at the insertion into the head capsule, to the apex;

SL – Scape length: length of the first antennal segment, excluding the neck and the basal condyle;

ED – Maximal diameter of the compound eye;

WL – Weber's length of the mesosoma (alitrunk): diagonal length, measured in lateral view, from the anterior margin of the pronotum (excluding the collar) to the posterior extremity of the metapleural lobe.

Identification of the parasite workers

It was not easy to distinguish between parasite and host minor workers, although the parasite workers have more abundant and dense pilosity on the gaster than do host minor workers. We distinguished host and parasite workers the same way Sumner *et al.* (2003) separated *A. echinatior* and *A. insinuator* workers based on the bulla of the metapleural gland in the parasite workers being smaller and further from the spiracle than in host workers. Thus, 300 minor workers ($\leqslant$ 5 mm) were randomly selected from three host colonies of *A. subterraneus subterraneus* for morphometric analysis. The measurements were taken using a Euromex binocular microscope computer, a Nikon Coolpix 4500 camera and the computer package Image Pro-Express to measure: (i) the shortest distance from the bulla edge to the nearest spiracle; and (ii) the width of pronotum.

Results

Acromyrmex ameliae sp.n. (Figs. 1, 3, 5, 7, 9–14)

Types Holotype queen labeled 'Brazil: Paraopeba MG/ 06 Oct 2003/ D. J. Souza' (MZUSP). Measurements (in mm): HL = 1.5; HW = 1.4; ML = 0.7; WL = 2.6; SL = 1.5; ED = 0.4.

Derivation of specific name This species is named after Amélia Maria de Souza, mother of the first author of this work.

Description The measurements obtained from 20 queens are presented in Table 1. This new species has a palpal formula of 4, 2 and 11 antennal segments as is typical for attine ants. *Acromyrmex ameliae* queens have large and convex eyes and the inferior pronotal spines are straight and forward-positioned as in the host species. The color of the analyzed parasite queens vary from brownish to brownish-black and this is not associated with the subspecies of host ants since one can find queens of the parasite of either color in a single nest. Worker color is the only character that is presently used to separate the two host subspecies: *A. subterraneus subterraneus* and *A. subterrraneus brunneus*. The latter has a brownish-black color whereas the former is light brown to yellow (Gonçalves, 1961). The queens of *A. ameliae* are much smaller than those of its hosts, with a WL ~ 0.6 as great (Table 1). *Acromyrmex ameliae* further has a more abundant pilosity with thicker and longer hairs on the gaster, on the dorsal portion of the alitrunk and on the anterior portion of the head, in comparison to that on the host subspecies. The parasite queen also has prominent ridges on the head (Figs. 1 and 2) and on the first segment of the gaster and expansions on the anteroventral margin of the post-petiole that are not seen on the host subspecies (Figs. 5 and 6). The tubercles on the gaster of *A. ameliae* are more or less ordinated in four longitudinal lines similar to the host species. However, these tubercles are very much reduced and less prominent when compared to those of the hosts.

Table 1 Head length (HL), head width (HW) and Weber's length (WL) for the social parasite *A. ameliae* and its hosts *A. subterraneus subterraneus* and *A. subterraneus brunneus*. All measurements are in mm.

	HL	HW	WL
Queens			
A. subterraneus subterraneus (*n* = 9, 6 nests)	2.1 ± 0.1	2.2 ± 0.2	4.0 ± 0.1
A. subterraneus brunneus (*n* = 8, 8 nests)	2.0 ± 0.1	2.1 ± 0.1	4.0 ± 0.1
A. ameliae (*n* = 20, 4 nests)	1.3 ± 0.1	1.3 ± 0.1	2.4 ± 0.1
Males			
A. subterraneus subterraneus (*n* =8, 7 nests)	1.3 ± 0.1	1.6 ± 0.1	3.1 ± 0.2
A. ameliae (*n* =15, 4 nests)	1.0 ± 0.1	1.2 ± 0.1	2.3 ± 0.7
Workers			
A. subterraneus subterraneus (only minor workers) (*n* = 16, 3 nests)	0.9 ± 0.1	1.1 ± 0.1	1.5 ± 0.1
A. ameliae (*n* = 30, 3 nests)	0.9 ± 0.3	1.1 ± 0.3	1.5 ± 0.1

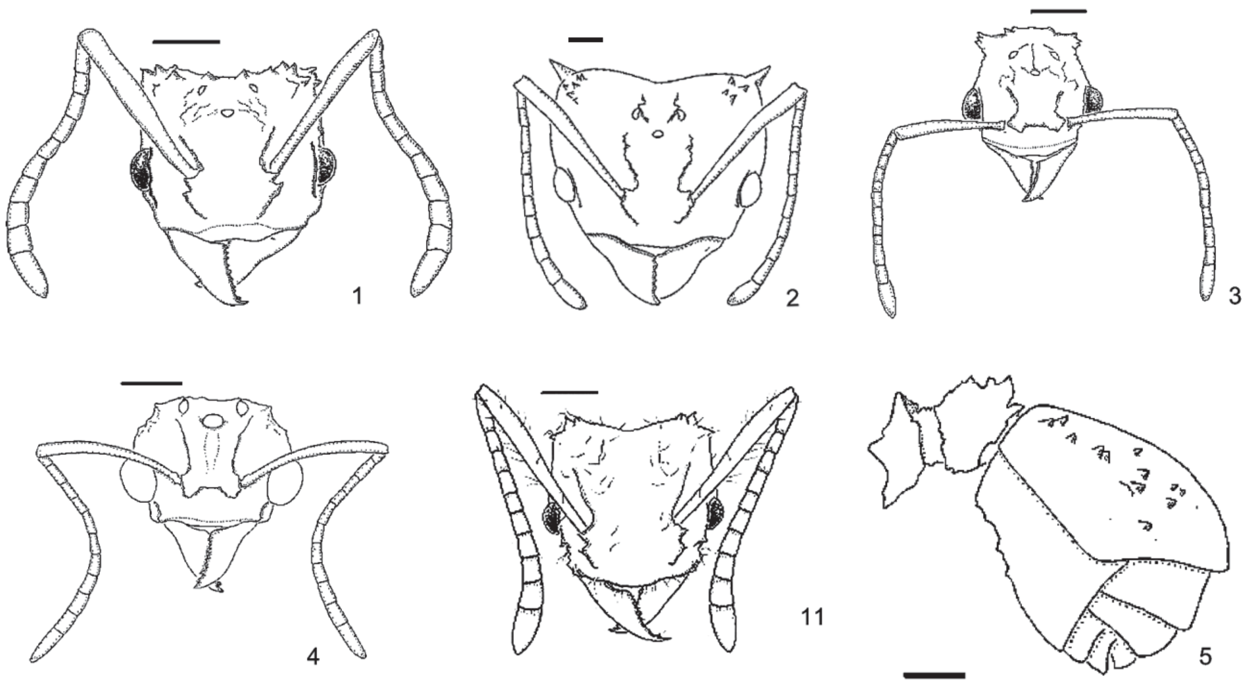
Paratype male labeled 'Brazil: Paraopeba MG/ 06 Oct 2003/ D. J. Souza' (MZUSP). Measurements (in mm): HL = 1.0; HW = 0.9; ML = 0.6; WL = 2.2; SL = 1.3; ED = 0.4.

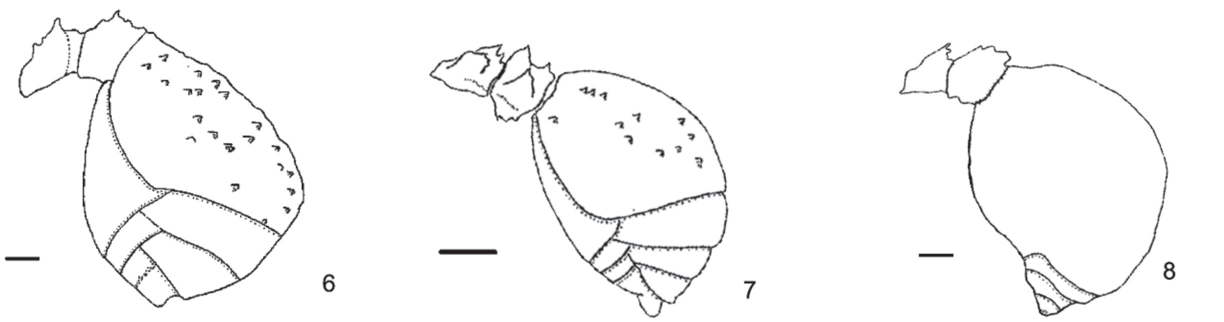
Description The measurements of 15 males are presented in Table 1. The males of *A. ameliae* have 13 antennal segments. This characteristic was not constant since five individuals seemed to have 12 segments as a consequence of the fusion of segments 4 and 5 of the antennal funiculum like in the host males (compare Figs. 3 and 4). This fact was also observed by Schultz *et al*. (1998) in *A. insinuator*. Males of *A. ameliae* are visually smaller than the males of the studied host species (about 1.2 times). The antenna has a color gradient which ranges from dark brown to dark yellow when going from tip to base. The color of the males as well as of the queens is close to that of the host subspecies *A. subterraneus subterraneus*, that is, very dark brown independent of the parasitized subspecies. However, as pointed out by Gonçalves (1961), the character color shows variation even inside the same nest. Newly emerged males and queens of *A. ameliae* of a lighter color were observed by the authors in the nests, but they became dark brown after a few days had elapsed. Their mandibles have a terminal tooth greater than the other teeth, which vary from 5 to 7 (Fig. 3). The ventral portion of the post-petiole of the parasite has irregular projections that are not seen in the host whose petiole margin is more regular and presents a concavity not observed on the parasite (Figs. 7 and 8). Ridges and tubercles can be observed on the gaster of *A. ameliae* males, but these are missing in the host species whose gaster is smooth and shiny.

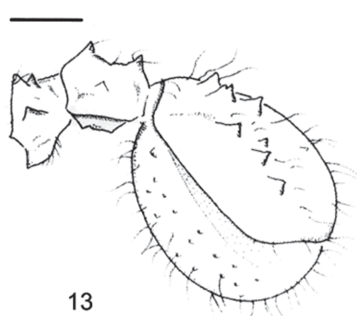
Paratype worker labeled 'Brazil: Paraopeba MG/ 06 Oct 2003/ D. J. Souza' (MZUSP). Measurements (in mm): HL = 0.6; HW = 0.7; ML = 0.3; WL = 0.9; SL = 0.8; ED = 0.1.

Description We verified that the distance from spiracle to bulla relative to pronotum width differed significantly among the minor workers of host and parasite ($F_{1,298} = 551.36$, $P < 0.01$). Two groups are clearly shown in Figure 15: one had a small number ($n = 25$) of parasite workers and another formed by a large number of host minor workers ($n = 275$). The fact that the workers sorted into two groups, as well as morphological differences between the groups, is highly suggestive. We found some *A. ameliae* workers are larger than host minors but this is because larger host minors were not sampled. Preliminary genetic analysis by RAPD (Random amplified polymorphic DNA) markers clearly shows differences between the two groups, confirming these results. As in *A. insinuator*, the workers of *A. ameliae* have a significantly smaller distance from their spiracle to bulla than their host minor workers of same pronotum width (Figs. 16 and 17). These results are almost identical to those obtained by Sumner *et al*. (2003) for *A. insinuator*.

Comments on biology There are previous reports on

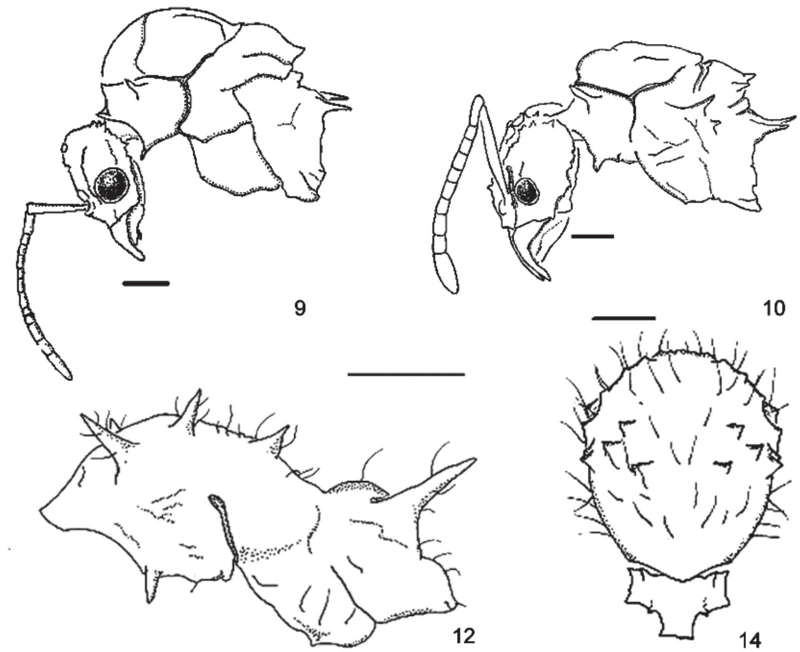






Figs. 1–4, 11 Frontal view of head of *Acromyrmex ameliae* queen (1), *Acromyrmex subterraneus subterraneus* queen (2), *A. ameliae* male (3), *A. subterraneus subterraneus* male (4) and *A. ameliae* worker (11). The bars correspond to a scale of 0.5 mm in figures 1− 4 and 0.25 mm in figure 11.
Figs. 5–8, 13 Lateral view of petiole, postpetiole, and gaster of *Acromyrmex ameliae* queen (5), *Acromyrmex subterraneus subterraneus* queen (6), *A. ameliae* male (7), *A. subterraneus subterraneus* male (8) and *A. ameliae* worker (13).

polygyny in the two host subspecies (Della Lucia & Vilela, 1989; Delabie, 1989). During nest collection, we indeed found three monoginic parasitized nests which had 2, 3 and 4 queens of *A. ameliae*. The first collection of the parasite was in October, 2003, when two nests were collected with hundreds of alate males and queens of the parasite. In April of the following year, we again collected nests with the alate parasites. This suggests that the production of the reproductive caste in *A. ameliae* may occur throughout the year. In the laboratory, males and queens flew towards the light, indicating that this species is likely to perform the nuptial flight in nature. As in *A. insinuator*, *Acromyrmex ameliae* produce a workforce. This seems to be essential for the production of the parasite alates (Sumner *et al*., 2003), but this trait is being selected against over evolutionary time, although it has not yet been lost. We need to investigate if the host cares for the parasite alates. In this case, parasite workers may not be needed.



Figs. 9–10, 12 Lateral view of head and metasoma of *Acromyrmex ameliae* male (9), *A. ameliae* queen (10), *A. ameliae* worker (metasoma only) (12). The bars correspond to a scale of 0.5 mm in figures 9–10 and 0.25 mm in figure 12.

Fig. 14 Dorsal view of gaster of *Acromyrmex ameliae* worker. The bar corresponds to a scale of 0.25 mm.

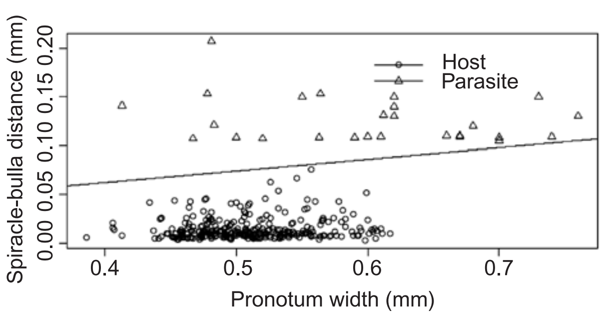
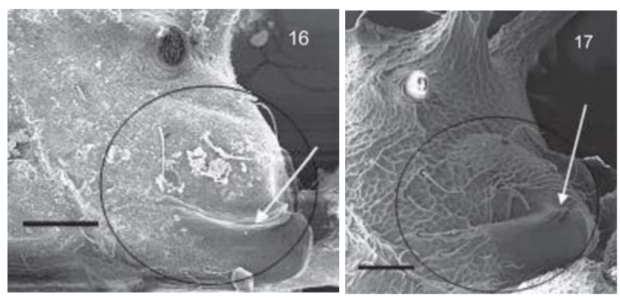


Fig. 15 The distance between the spiracle and the bulla as a function of the pronotum width for minor workers of *Acromyrmex subterraneus subterraneus* and *Acromyrmex ameliae* ($F_{1,298}$= 551.36, $P < 0.001$).



Figs. 16–17 Scanning electron micrograph of the mesosoma of *Acromyrmex subterraneus subterraneus* (16) and *A. ameliae* (17), showing the large pronounced vault (bulla) which covers the storage chamber. Arrows point to the slit-shaped opening (meatus). The bulla in host worker is closer to the spiracle than in parasite workers. The bars correspond to a scale of 100 μm.

Paratypes 20 queens, 20 males and 18 workers. Labeled 'Brazil: Paraopeba MG/ 20 April 2004/ I. M. F. Soares (MZUSP).

Discussion

Acromyrmex ameliae is a social parasite with much smaller reproductives (females and males) than those of its hosts (Table 1). Morphometrically, the *A. ameliae* queen is not a simple miniature of its hosts' queens, like *Myrmica microrubra* and its host *Myrmica rubra* (Steiner *et al.*, 2005). Here, we can distinguish the new species from the other of the group with propodeal spines: they are straight and laterally compressed unlike *subterraneus* subspecies where they are slight to strongly curved and conical. *Acromyrmex ameliae* differs from *A. insinuator* not only by its size (compare Tables 1 and 2) and color (brown dark against yellowish-orange) but as well it does not present a single strong median ruga extending from the central ocellus to the level of the posterior borders of lateral ocelli, like *A. insinuator*. On the contrary, around its central ocellus, the cuticle is wholly rugous without a distinct median ruga. In *A. insinuator* the anteroventral edge of the postpetiole is broadly and evenly concave, without a broad median anteroventral extension. The anteroventral portion

Table 2 Head length (HL), head width (HW) and Weber's length (WL) for the social parasite *A. insinuator* and its host *A. echinatior* (Schultz *et al.*, 1998).

	HL (mm)	HW (mm)	WL (mm)
Queens			
A. echinatior (n = 11, 9 nests)	2.2 ± 0.1	2.6 ± 0.2	3.8 ± 0.1
A. insinuator (n = 25, 5 nests)	1.9 ± 0.1	2.3 ± 0.1	3.3 ± 0.2
Males			
A. echinatior (n = 12, 11 nests)	1.4 ± 0.1	1.8 ± 0.1	3.5 ± 0.3
A. insinuator (n = 18, 5 nests)	1.4 ± 0.1	1.6 ± 0.1	3.0 ± 0.2

of the post-petiole in *A. ameliae* has irregular extensions, without the concavity present in the first species.

As in *Acromyrmex insinuator*, reproductives (females and males) *A. ameliae* very much resemble the host species, although there has been a pronounced reduction in body size. From observations of nuptial flights that occurred in the laboratory, we can suspect that a mating flight occurs in the field. However, observations of nuptial flights in the field are necessary to conclude this. We found alate parasites in two different seasons (April and October), unlike the host species, which has only a single synchronized nuptial flight per year in November and December. More than one nuptial flight each year could increase their likelihood of successful invasion of new colonies. The well defined nuptial flight of the hosts is normally observed in November and December so that newly fertilized parasite queens (produced in April) can colonize established colonies of *A. subterraneus subterraneus* and *A. subterraneus brunneus* well before they reproduce themselves. We suggest that further studies should investigate the chemical profile of the involved species to answer the following questions. Does the newly fertilized parasite queen lack external chemical substances, as hypothesized by Lenoir *et al*. (1999)? Is there an absence of colony specificity in hydrocarbons composition among hosts and parasite species? The chemical ecology of interactions between ants and their social parasites exhibits a potential field for research since it constitutes a multiplicity of complex interactions, yet it has been little studied (Lenoir *et al*., 2001).

Like *A. insinuator* (Bekkevold & Boomsma, 2000), *A. ameliae* is one of the rare inquiline parasites that produces workers and resembles its host in morphology, but unlike *A. insinuator*, *A. ameliae* queens differ dramatically from their host queen in size. We excavated 14 colonies of *A. subterraneus* and found all of them parasitized by *A. ameliae*. Thus, *A. ameliae* appears to be very common, yet always overlooked in the past. Perhaps many other similar social parasites await discovery.

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