

Research article

Nest architecture and colony size of the fungus-growing ant *Mycetophylax simplex* Emery, 1888 (Formicidae, Attini)

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Abstract. Detailed measurements on nest architecture and colony size of the fungus-growing ant *Mycetophylax simplex* Emery, 1888 (Formicidae, Attini) are reported for the first time, based on excavations of 55 nests from two sites in southern Brazil. All nests were subterranean, with a single entrance hole. Most nests consisted of two chambers, an upper and a lower chamber, but one and three-chamber nests were also found. The chambers were more cone-shaped than rounded, and located at a depth ranging from 4.0 cm to 32.5 cm below the nest entrance. The chamber dimensions generally increased as the depth of the chambers increased, and the lower chamber was mostly wider than the upper one. The fungus garden was always found resting on the chamber floor. The average colony size was 264.1 workers, ranging from 67 to 610 workers. Colonies produced most sexuals during the summer (from December to March) and a few during the winter (July). Direct observations showed that colonies were mostly monogynous, but more than one queen was recorded in two nests, suggesting that polygyny may also occur in this species.

Keywords: *Mycetophylax simplex*, Myrmicinae, Attini, fungus-culturing ants, ant nests.

Introduction

Nest architecture of social insects, including termites, social wasps and bees has received considerable attention. These structures have been recognized as frozen portrayals of behavior because they are manifestations of behavior (Sudd and Franks, 1987). Ant nests, in contrast, are more poorly known, due in part to being less accessible since they are usually subterranean (Hölldobler and Wilson, 1990; Tschinkel, 2003).

In general, the architectural components of subterranean ant nests are relatively simple, but the overall structure can differ in volume, complexity and form among species (Hasiotis, 2003; Tschinkel, 2003). Several attempts have been made over the years to obtain casts of the underground structure of ant nests (Williams and Lofgren, 1988). Unfortunately, descriptions of ant nests have become less common in recent years, since they are not usually the primary objective of most reports. Nevertheless, nest architecture can structure social interactions and nest size and morphology are often diagnostic at the species level (Tschinkel, 2003).

The tribe Attini belongs to the subfamily Myrmicinae and comprises twelve genera of fungus-growing ants (Kempf, 1972), all of which occur exclusively in the Americas (Weber, 1982; Hölldobler and Wilson, 1990). Excluding the monospecific workless parasite *Pseudoatta* not studied, the attines have traditionally been divided into two groups: the higher attine clade (Attoid) contains the well-known leafcutter ants (*Atta* and *Acromyrmex*) as well as other, non-leaf-cutting genera (*Sericomyrmex* and *Trachymyrmex*). The remaining attines species belong to the so-called lower attine clade (Apterostigmoid), of which three genera (*Myrmicocrypta*, *Mycocepurus*, and

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Apterostigma) form a basal monophyletic clade, and four genera (*Mycetarotes*, *Mycetosoritis*, *Cyphomyrmex*, and *Mycetophylax*) comprise an intermediate clade (Schultz and Meier, 1995).

The intermediate clade of attines occupies a critical position for understanding the evolution of this fascinating group of ants. However, most studies to date on nest architecture, nesting and reproductive biology of the fungus-growing ants have been concerned with those genera considered pests: *Atta* and *Acromyrmex* (e.g. Mariconi, 1970; Weber, 1982; Diehl-Fleig and Lucchese, 1992; Diehl-Fleig and Araújo, 1996; Moreira et al., 2004a,b). The biology and ecology of the other attine genera remain poorly known (Fernández-Marín et al., 2004). The “lower” Attini, have perhaps been overlooked due to their lack of aggressiveness, cryptic behavior and inconspicuous nests, which make field observations difficult (Weber, 1982; Mayhé-Nunes, 1995, Fernández-Marín et al., 2005). Only recently have detailed nest architecture descriptions became available for *Cyphomyrmex longiscapus* (Mueller and Wcislo, 1998), *Trachymyrmex septentrionales* (Tschinkel, 2003), *Mycetarotes acutus*, *Mycetarotes carinatus* and *Mycetarotes parallelus* (Solomon et al., 2004) and for *Mycocepurus smithii* (Fernández-Marín et al., 2005).

The genus *Mycetophylax*, consisting of nine species (Kempf, 1972), is commonly found in arid zones of extra-tropical South America. The origins of the attine symbiosis are thought to have occurred in a wet tropical environment; therefore, *Mycetophylax* represents one of several adaptive radiations of attine ants in an arid environment (Mayhé-Nunes, 1995). One species, *Mycetophylax simplex* is quite common in the mobile sand dunes of the Atlantic coast in southern Brazil (Rio Grande do Sul State). Nevertheless, its biology and ecology are almost completely unknown, with only one recent publication on this species (Albuquerque et al., 2005). We evaluated two populations of *M. simplex* in the coastal sand dunes in northern Rio Grande do Sul state, made detailed measurements of nest architecture, estimated the colony sizes, determined the period of alate production, and the period of foraging activity for this little-known attine species.

Materials and methods

Ant collections and observations of foraging activity period of *M. simplex* were carried out at two sites in the municipality of Torres, northern Atlantic coast of the Rio Grande do Sul state, southern Brazil, from October 1997 to September 1998. One of the sites is located in the Praia Grande beach (29°20'S; 49°43'W), on a narrow of remnant sand dunes between the shore and the urban area. The climate is characterized as subtropical. The mean monthly temperature ranges from 19°C in July (winter) to up 35°C in January (summer) with an annual mean temperature of 24°C (www.torres.com.br/cidades.htm). The annual rainfall is 1.200 mm, with a slight accumulation in November and December (Cordazzo and Seeliger, 1995).

The dune vegetation is very scarce, mostly interrupted by marshes (Rambo, 1954) and limited to few species, mainly of crawling and

pioneer plants. The other site is located behind the Morro da Guarita hill (29°21'S; 49°44'W) in a suburban area not far from the seashore. The soil is sandy and plant cover is sparse and mainly composed of introduced species of grasses.

The nests (N = 55) were located by following foraging workers back to their nests, which were then marked. Only nests presenting more than ten foraging workers were considered to be established nests, and were therefore marked and subsequently excavated. Previous observations have indicated the activity period of *M. simplex* as largely nocturnal, therefore, nest locations were identified during the night, while nest excavations were performed in the period of inactivity (during the day) of the ants. For nest excavations, a 40.0 – 50.0 cm pit was dug at a distance about 15.0 cm from the nest entrance so as not to destroy the nest. The excavation proceeded laterally toward the nest until the chambers were encountered, each of which was exposed one at a time (according to Tschinkel, 1987).

For 47 of the 55 nests, we observed the following aspects: presence or absence of sexuals, shape of the crater surrounding the entrance hole, presence or absence of a turret at the entrance, and number of entrance holes. For the other eight nests, we counted the number of all mature individuals and the number of chambers, and, with the exception of one nest, we measured the following characters: chamber depth (distance from the entrance to chamber floor), chamber height (greatest distance from floor to ceiling), chamber width (greatest horizontal diameter), diameter and length of the tunnel connecting the chambers. A schematic representation of the nest architecture was drawn based on average measurements of the seven nests.

The fungus garden and all the individuals found in each chamber of the eight nests were collected and the workers, queens, males and gynes were counted as an estimate of the colony size. Voucher individuals were deposited in the Formicidae Collection of the Laboratory of Social Insects of the University of Vale do Rio dos Sinos – UNISINOS, São Leopoldo, Rio Grande do Sul (Brazil) and at the Zoological Museum of the University of São Paulo – MZUSP, São Paulo, SP (Brazil).

Results

All the 55 observed nests of *M. simplex* were subterranean, with a single entrance hole. In 24 of the 55 nests (43.6%) the entrance was located on the top of a small, well-defined sand turret, and the remnants of a surrounding crater were also visible. In the other 31 nests (56.4%), the entrance was located centrally in the bottom of a small crater made of excavated soil. Two to three chambers (2.1 mean), generally, were found per nest, but one chamber nest also occurs (Figures 1 and 2). The chambers were more cone-shaped than rounded and were located between 4.0 cm to 32.5 cm below the surface and between 2.0 cm to 33.0 cm laterally to the nest entrance. A single tunnel 1.5 cm to 12.5 cm long connected the chambers, with a minimum and maximum diameter of 3.0 mm and 5.0 mm, respectively.

The dimensions of the chambers varied greatly, ranging from a minimum height of 2.0 cm to a maximum height of 10.0 cm. The minimum and maximum widths were 1.5 cm and 19.0 cm, respectively (Table 1).

In the eight evaluated colonies, a minimum of 68 individuals (67 workers and a queen) and a maximum of 611 individuals (610 workers and a queen) were found. In two of these colonies, two and six dealate females were observed in each one. In the summer (December to March) males and gynes were found in four of the eight

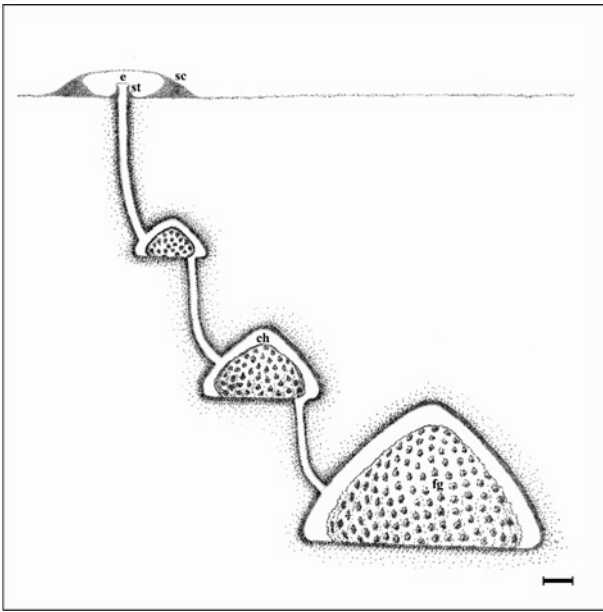


Figure 1. Scheme, in transversal section, of the architecture of the subterranean nests of *Mycetophylax simplex*: e, entrance; st, sand turret; sc, sand crater; t, tunnel; ch, chamber; fg, fungus garden (bar represents 2 cm).

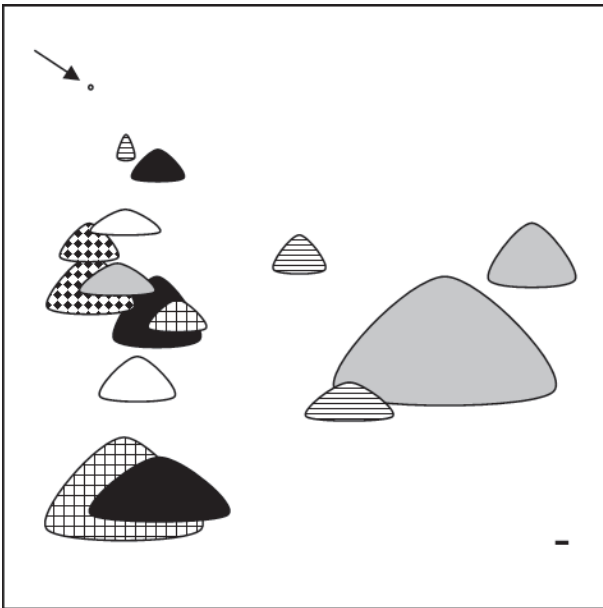


Figure 2. Scheme, in transversal section, of six subterranean nests of *Mycetophylax simplex* (Formicidae, Attini) all aligned by the nest entrance hole, with the chambers from the same nests represented with the same color pattern (bar represents 1 cm; arrow points the nest entrance).

evaluated colonies (Table 2), and in 22 (56.4%) of the other 47 excavated nests. In a nest of *M. simplex*, one male and some gynes were observed around the entrance in July (winter).

The workers were generally present in all chambers, and the queen was usually observed in the deepest

chamber. Males and gynes occupied the two deepest chambers (Table 2). The fungus gardens were located in all chambers, although in some nests it was absent in the highest chamber. The fungus garden usually filled nearly the entire chamber.

The entrance hole of the nests were always closed with sand from 7.00 AM to 3.00 PM. Around 4:00 PM ants started removing the sand from the nest entrance and from 9:00 PM to 5:00 AM intense foraging activity was observed, which correspond to night period. The observed workers foraged only on dry grass fragments, never cutting live plants. In the fungus garden dry grasses and small seeds, but no corpses, feces or insect parts were found.

Discussion

All of the nests of *M. simplex* were subterranean, as is typical in arid regions (Kaspari, 2000). The nest entrances of *M. simplex*, with an entrance hole surrounded by a sand crater or located on the top of a small sand turret, are similar to those described by Weber (1982) for *Mycetophylax conformis*. The crater and the turret may prevent sand from entering the nest during windy periods or when dunes shift. Lopes (2001) refers larger craters (mean height 1.57 cm and mean diameter 4.77 cm) are constructed by *Cyphomyrmex morschii* in a site of sand dunes in the Atlantic coast of southern Brazil (Santa Catarina State), which could provide protection in the same way. Wind speed or rain prior to the observations could explain some of the variation found in the external appearance of the nests, specifically the presence or absence of craters, as has been reported for a few nests of *C. morschii* (Lopes, 2001). While nests consisting of craters are more frequent among ant species in tropical or arid zones, nests with mounds covering the entrance are more common in colder areas, as this architecture acts like a heater by increasing the surface area of the nest exposed to sunlight (Sudd and Franks, 1987; Lopes, 2001). However, the subterranean nest architecture of *M. conformis*, as described by Mayhé-Nunes (1995), differs from our observations of *M. simplex*. The architecture and structure of the ant nests can be influenced by the type, texture and humidity of the soil (Kaspari, 2000; Halley et al., 2005), which could explain some of the differences found in the nest architecture between *M. conformis* and *M. simplex*.

Chamber dimensions of *M. simplex* nests varied, with an increase in depth generally correlated with an increase in the height and width of the chambers such that lower chambers were wider than the upper ones. In two of the eight nests of *M. simplex* the first chamber was empty and in two other nests only a few workers were found in the first chamber. According to Solomon et al. (2004), in some lower attine species the uppermost chambers are abandoned as the colony grows and new, deeper chamber are constructed. In one of the eight excavated nests, the first chamber contained a few workers and a large number of unidentified seeds were

Table 1. Size of the chambers (cm) of seven nests of *Mycetophylax simplex* (Formicidae, Attini) excavated in the sand dunes of the Atlantic coast in southern Brazil (Torres, Rio Grande do Sul State).

Nest	First Chamber			Second Chamber			Third Chamber		
	Depth ¹	height ²	width ²	depth ¹	height ²	width ²	depth ¹	height ²	width ²
1	4.00	2.50	nm	8.50	4.50	nm	–	–	–
2	7.00	2.50	4.50	19.50	5.50	7.50	32.50	5.00	12.00
3	13.00	3.00	5.00	17.00	4.50	7.50	–	–	–
4	11.00	2.00	6.00	23.50	3.50	6.50	–	–	–
5	18.20	2.50	5.00	34.00	8.00	13.50	–	–	–
6	15.50	2.50	6.50	15.00	5.00	7.50	24.00	10.00	19.00
7	5.50	2.00	1.50	14.00	3.00	4.50	25.00	3.00	7.50
Average (±s.d.)	10.60 (±5.32)	2.43 (±0.35)	4.75 (±1.75)	18.79 (±8.16)	4.86 (±1.62)	7.83 (±3.01)	27.17 (±4.65)	6.00 (±3.61)	12.83 (±5.80)

¹ distance from the nest entrance to the chamber floor; ²maximum values; nm: not measured.

Table 2. Colony size and distribution of the individuals in eight colonies of *Mycetophylax simplex* (Formicidae, Myrmicinae, Attini) in the sand dunes of the Atlantic coast in southern Brazil (Torres, Rio Grande do Sul State).

Nest	Chamber			Number of individuals				
	First	Second	Third	W	M	G	Q	Total
1	F, W	F, W, G, Q	–	69	0	6	1	76
2	F, W	F, W, Q	F, W, M, G, Q	160	4	32	6	202
3	F, W	F, W	–	160	0	0	0	160
4	W	F, W	–	90	0	0	0	90
5	Empty	F, W, M, G, Q	–	266	7	85	2	360
6	W	F, W, M, G	F, W, M, G, Q	228	140	189	1	558
7	Empty	F, W, Q	F, W	610	0	0	1	611
8	F, W	F, W, Q	–	67	0	0	1	68

¹ F, fungus garden; W, worker; M, male; G, gyne; Q, queen.

found, suggesting that the chamber may act as a storage room for material that has not yet been incorporated into the fungus garden.

The basic structure and subterranean architecture of the nests of *M. simplex* are quite similar to the pattern observed for many species of other attine genera, that is, soil-built nests containing one or more chambers. However, the colony sizes are very different such as in *Acromyrmex* and *Atta* (e.g. Gonçalves, 1961; Mariconi, 1970; Weber, 1982; Diehl-Fleig and Droste, 1992). Many of the lower-attine species such as *M. smithii* (Fernández-Marín et al., 2005) construct multiple chambers in a vertical series, while the nests of *Mycetarotes* spp. often consist of only a single chamber, occasionally with a second chamber (Solomon et al., 2004). Recently, Klingenberg (2006) described the nests of *M. simplex* with only one fungus chamber at about one meter below the surface in the sand dunes of the Atlantic coast of Santa Catarina State. The differences found between *M. simplex* nests described by Klingenberg (2006) and the nests we observed might be due to different geographic locations where the studies were carry out. The main differences among the several attine nests include num-

ber, volume, and depth of the chambers, and could partly result from differences in the size of the colony of each species, as suggested by Tschinkel (1999, 2003) and Hasiotis (2003) for other ant species. Halley et al. (2005) refer that the pattern of nest growth in *Linepithema humile* as a process of density-dependent stimulation of excavation, which subsided as nest grew and the density of digging stimuli declined. Thus, nest excavation would be auto-regulating, and final nest size should be proportional to colony size. The nest architecture and population structure also can be influenced by habitat conditions such as soil type (Hölldobler and Wilson, 1990), in which ants dig (Halley et al., 2005).

The fungus garden of the nests of *M. simplex* was located resting on the floor of the chambers, as was also reported for *M. conformis* (Weber, 1982; Mayhé-Nunes, 1995) and many other attine species (Gonçalves, 1961; Mariconi, 1970; Weber, 1982; Mayhé-Nunes, 1995; Mueller and Wcislo, 1998; Fernández-Marín et al., 2004). In contrast, in the nests of *Acromyrmex octospinosus*, *Trachymyrmex bugnioni* (Fernández-Marín et al., 2004), *M. acutus*, and *M. parallelus* (Solomon et al., 2004) the fungus gardens were found suspended from rootlets

hanging within the chambers. In established colonies of *Mycocrepurus smithii* the fungus garden was suspended directly from the surface of the chamber ceiling (Fernández-Marín et al., 2005). For some of the *M. simplex* nests we observed, the fungus garden was absent in the most superficial chamber, possibly resulting from the unfavorable conditions for the symbiotic fungus created by the high temperatures and low humidity found right below the soil surface (Kusnezov, 1963; Weber, 1982).

The foraging activity of *M. simplex* colonies was mainly observed at night when the temperature is not too high, reducing the susceptibility of dehydration of the workers (Hölldobler and Wilson, 1990). Similar to what has been reported for *M. acutus* and *M. parallellus* (Solomon et al., 2004), the foraging substrates used to cultivate the fungus garden of *M. simplex* consisted primarily of vegetative materials, including grass bits, leaf fragments, buds and seeds; no arthropod corpses, feces, pieces of insects or other invertebrates were found. For *M. conformis* and other lower-attine species, however, the fungus substrate includes dead vegetable matter, feces and pieces of insects (Weber, 1982; Mayhé-Nunes, 1995; Leal and Oliveira, 2000; Fernández-Marín et al., 2005).

The great variation in the number of workers (67 – 610; 264.1 mean) in the nests of *M. simplex* could be due to variety in colony age, as has been suggested by some authors (Mariconi, 1970; Weber, 1982; Hölldobler and Wilson, 1990; Solomon et al., 2004). However, the maximum number of workers was not different from that reported for *M. conformis* (Weber, 1982). Recently, Klingenberg (2006) reported a minimum and a maximum of 33 and 535 workers (245 mean) in the nests of *M. simplex*, respectively. The minimum and mean numbers of workers found by Klingenberg (2006) are lower than our numbers, perhaps resulting from colonies age of the studied populations. Solomon et al. (2004) reported an estimate of 20 to 30 workers from one nest of *M. acutus*, and five to 258 workers (111 mean) in the nests of *M. parallellus*, while Fernández-Marín et al. (2005) reported a mean of 77 workers in the nests of *M. smithii*. The colonies of *M. simplex* had more workers than these other lower attines and far less than the more derived genera *Acromyrmex* and *Atta*. Our results are therefore consistent with the suggestion of some authors that refer to *Mycetophylax* as an intermediate genus of Attini (Hölldobler and Wilson, 1990; Mayhé-Nunes, 1995; Leal and Oliveira, 2000).

The presence of more than one dealate female in two of the eight evaluated nests suggests the possible occurrence of polygyny in *M. simplex*, as has been reported in some *Acromyrmex* species (Diehl-Fleig, 1995; Diehl-Fleig and Araújo, 1996; Diehl et al., 2001), and *Atta texana* (Mintzer, 1987). However, many attine species can occasionally retain dealate females in the nest, but these females generally function as workers (Weber, 1972). This could be the case of supernumerary dealate females observed in the nests of *M. simplex*. For *M. smithii* one to more than five dealate females were observed in established nests (Fernández-Marín et al., 2005), but the authors did not state whether they were queens or dealate

gynes. In a small fraction of nests of *C. longiscapus* one can find supernumerary dealate females (Mueller and Weislo, 1998), but they do not function as queens (Mueller, pers. comm.).

The newly emerged reproductives found in some nests from December to March indicated that the period of sexual production of *M. simplex* is in the summer (dry season in southern Brazil), as has been reported for several species of *Acromyrmex* (Diehl-Fleig, 1993, 1995). However, for the majority of Neotropical attine ants, such as *Atta* spp. (Mariconi, 1970; Weber, 1982; Hölldobler and Wilson, 1990) and *M. smithii* the annual production of new alates and nuptial flights occurs during the rainy season (Fernández-Marín et al., 2005). The presence of a male and several gynes in one nest of *M. simplex* in July (winter) could suggest another period of alate production such as reported for other ant species. The existence of more than one period of maturation of the sexual brood could have an adaptive value since an entire brood may be destroyed by a local catastrophe (Sudd and Franks, 1987; Hölldobler and Wilson, 1990).

Nest architecture of soil-dwelling social insects is an important source of data for understanding the evolution of social behavior of this insect group (Hasiotis, 2003; Tschinkel, 2003), especially because nest building is the collective product of the efforts of many individuals (Sudd and Franks, 1987; Hölldobler and Wilson, 1990). The range of extant nest architectures of several types of solitary to social insects and key features in their architecture are important tools in the identification of their structures in the geologic record. A deeper knowledge of the mechanism of formation, function and structure of extant ant nests would be helpful for recognizing and understanding ichnofossil ant nests. Study of such fossil registers might shed light on the evolution of ant social behavior, as well as the paleoecological conditions in which ants evolved (Tschinkel, 2003). We hope that this study on the architecture and colony size of nests of *M. simplex* can be used as a helpful tool to ant ichnology, as well as to aid in the understanding of the biology and evolution of the tribe Attini.

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