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Research article

Nest architecture of the leaf-cutting ant *Acromyrmex rugosus rugosus*

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Abstract. The prominent nests mounds of many ant species are one of the most obvious signs of their presence, yet the subterranean architecture of nests is often poorly known. The present work aimed to establish the external and internal structure of nests of a species of leaf-cutting ant, *Acromyrmex rugosus rugosus*, by either marking the interior of nests with talcum powder, or forming casts with cement. Twelve nests were excavated and surveyed, with eight being marked with talcum powder and four cast with cement. The external and internal structure of the nests was highly variable. The largest and smallest nests had mound areas of 9.89 m^2 and 0.01 m^2 respectively. The number of chambers found ranged from 1 to 26, with maximum dimensions of between 6 and 70 cm. Chambers were found close to the soil surface (6 cm) down to a maximum depth of 3.75 m. In addition to chambers containing fungus garden, some chambers were found to be empty, filled with soil or filled with waste, the first time this has been recorded in a species of *Acromyrmex*. The nests of *A. rugosus rugosus* appear to be unusually complex for the genus, containing a diversity of irregular chambers and tunnels.

Keywords: Attini, waste management, nest cast, myrmecophiles.

Introduction

Nest structure is a key factor in the survival of ant colonies. Nests serve to protect the vulnerable brood and queen(s) from natural enemies and other dangers, and also aid the maintenance of optimal microclimatic conditions for colony growth (Sudd, 1982). The nest represents a significant investment of energy for a colony that cannot be recuperated in the manner of some other investments, such as brood which can be cannibalized if necessary. In *Formica pallidefulva*, for example, it has been estimated that if a colony moves twice per year then it spends 20 % of its energy on the construction of nests (Mikheyev and Tschinkel, 2004). The fact that so much energy is invested in nests is indicative of the significance of the benefits that they bestow on their colonies. Consequently, ants show a wide diversity of species-specific nest designs that range from simple to highly complex, and which may be arboreal, in cavities, on the ground surface, or, in most taxa, subterranean (Hölldobler and Wilson, 1990; Theraulaz et al., 1998). Of these, subterranean nests are particularly hard to study and the architectural details are poorly known for most species (Tschinkel, 2004).

The nests of leaf-cutting ants (*Atta* and *Acromyrmex*) are a striking feature of the Neotropical region. Leaf-cutting ants are well known as being ecologically important because of the large quantities of vegetation that they harvest as a substrate for their mutualistic fungal food (Weber, 1972), something that also makes them significant pests of agriculture (Mariconi, 1970; Forti, 1985; Fowler et al., 1986; Hölldobler and Wilson, 1990). What is less often appreciated is the other ecological effect that they have as soil modifiers though nest building, which alters the chemical and physical properties of the soil, promotes the cycling of nutrients and favors the growth of plants (Haines, 1983; Coutinho, 1982; Moutinho et al., 2003). It is because of their effects on soil as well as their herbivory that they can be considered keystone species in many ecosystems (Fowler et al., 1989).

The nests of *Atta* and *Acromyrmex* have very different structural characteristics (Hölldobler and Wilson, 1990). Mature nests of *Atta* spp. may contain more than seven thousand subterranean chambers, linked to each other and to the soil surface by tunnels (Jacoby, 1950; Jonkman, 1980; Moreira et al., 2004a). Nests of *Acromyrmex* spp., in contrast, are generally small with only one or a few chambers (Gonçalves, 1961, 1964; Fowler, 1979). Above ground, nests of *Atta* spp. are characterized by one or several mounds of loose soil extracted from within the nest, whereas such mounds may or may not be present in *Acromyrmex* spp. (Autuori, 1942; Forti, 1985; Moreira et al., 2004a, b). There is also much variation within the genera, and differences in the structure of the mound can sometimes be useful in the identification of species (Gonçalves, 1967; Pacheco and Berti-Filho, 1987; Forti et al., 2006).

The most reliable method of examining the subterranean structure of ant nests is by casting the interior, and various substances have been used for this such as dental plaster, and molten zinc or aluminum (Tschinkel, 2003, 2004, 2005; Mikheyev and Tschinkel, 2004; Halley et al., 2005). Nests of *Atta* spp. have been unusually well studied using this technique, with cement being the most commonly used substance for casting (Jacoby, 1935, 1950; Moreira et al., 2004a,b; Andrade et al., 2005). However, no casting studies have previously been attempted for *Acromyrmex*. In this study we use the casting technique to study the nest architecture of one *Acromyrmex* species, *A. rugosus rugosus*, which nests in areas of grassland and disturbed habitat. *Acromyrmex* species cluster into two clades matching their geographical distributions (Sumner et al., 2004), and *A. rugosus* is a member of the South American clade.

Materials and methods

Twelve *A. rugosus rugosus* nests were studied between 2003 and 2005 in Botucatu, SP, Brazil (22°53'09''S; 48°26'42''W). For each nest, the width and length of the nest mound(s) was measured and the mound(s) photographed. Entrance holes were detected and counted by blowing talcum powder into one entrance hole of the nest with a manual pump and then observing the egress of the powder from any other entrances. Two lengths of string were then stretched perpendicularly over the mound to act as references for mapping the chambers and tunnels.

For nests 1–8, talcum powder was used to mark the internal structure by pumping it into the nests. The internal structure of the other four nests (9–12) was cast with a suspension of cement and lime (2 kg of cement and 1 kg of lime in 10 l of water) that was poured into the nest entrances following the methodology of Jacoby (1935). Nests were excavated immediately after marking with talcum powder or one week after casting with cement. In each case, a ditch was dug around the nest and this was then excavated inwards and downwards according to the appearance of chambers and tunnels. The depth, length, height and width of chambers were recorded for all nests, and the diameter and length of tunnels were recorded for the nests filled with cement. In addition for the nests marked with talcum powder, the contents of chambers (fungus garden, soil or waste material) were removed, transported to the laboratory in pots or plastic sacks so as to minimize water loss, and the volumes estimated using a graduated cylinder. Subsamples (10% by volume) of waste material were then examined for macroorganisms using the Berlese funnel technique, with subsamples being left under a 25 w lamp for seven days.

Spearman Rank Correlation Coefficients were used to examine the relationships between the four main nest attributes measured: area of nest mound, number of entrance holes, number of chambers and maximum depth. We tested whether the number of chambers found differed between the two casting methods used (talcum powder or cement) by means of an ANOVA with nest mound area included as a covariate to control for nest size. Whether the depth of chambers was normally distributed was checked with a Kolmogorov-Smirnov test. Finally, we also examined whether the depth of chambers was associated with their contents using a Kruskall-Wallis test.

Results

Although the nests of *A. rugosus rugosus* were found in various habitats, including fields and urban areas, they were observed to be located most frequently in locations that made excavation difficult: next to buildings or trees, or on inclines. When next to trees, fungus chambers were often found interwoven with tree roots, and on occasion roots were used as tunnels or chambers (Figs. 1 and 2). The mother queen was located for colonies 1, 2, 4, 5 and 8. She was found, together with brood, in the only fungus chamber of the former three colonies, and in the chamber with the largest volume of fungus in the latter two colonies. Winged males and gynes were found in nests 7 and 12, confirming that these colonies were mature.

Nest architecture

Externally, nests of *A. rugosus rugosus* had between one and 11 entrances, most of which were at the centre of one or more loose mounds of soil. The mounds were irregularly shaped, consisting normally of scattered, half-moon craters, but being compacted when the colony was located in a pasture, and ranged from 0.01 to 9.89 m^2 (Table 1; Figs. 1 and 2). Nests contained between one and 26 chambers that either contained fungus garden, soil, waste material or were empty (Table 1; Figs 2 and 3). The number of chambers found did not differ significantly between the two marking methods used (talcum powder or cement) when nest size was taken into account ($F_{1,9} = 2.29$, $p = 0.165$). Chambers irregularly distributed (Fig. 1), rather than being arranged in a simple, consistent manner (e.g. vertically arranged on the shaft of the same tunnel). Most chambers though, were generally either directly below or very close to the surface mounds and this was always the case for fungus chambers (Fig. 1). Chamber depth ranged from 6 cm to 3.75 m and was not normally distributed ($Z = 1.57$, $p = 0.015$), with the number of chambers decreasing with increasing depth (Fig. 3). All but three chambers were less than 2 m deep, while all the chambers in the four small nests (1–4) were no more than 0.27 m deep (Fig. 3). The types of chambers differed significantly in

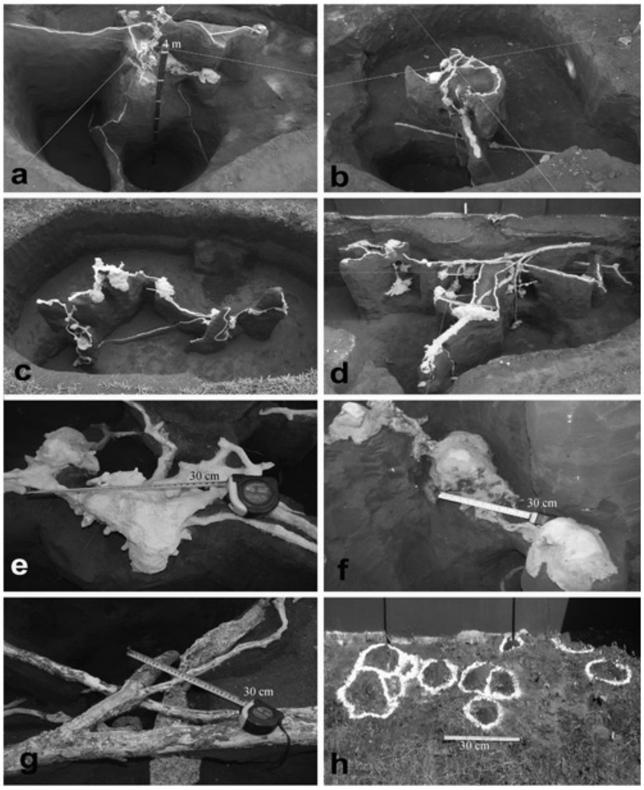

Figure 1. Three-dimensional view of *Acromyrmex rugosus rugosus* nests cast with cement (**a, b, c** and **d**). (**a**) Nest 9 reaching a depth of 3.75 m. (**b**) Nest 10, a smaller nest with a mound area of 0.27 m^2. (**c**) Nest 11 located in pasture. (**d**) Nest 12, the largest nest in terms of number of chambers (26) and mound area (9.89 m^2). (**e**) Detail of chamber showing multiple protuberances interconnected by various tunnels. (**f**) Detail of chambers without protuberances and connected by only a single tunnel. (**g**) Detail of tunnel arrangement, showing old roots being utilized as tunnels. (**h**) General view of the external mounds of nest 12 which was located next to a building.

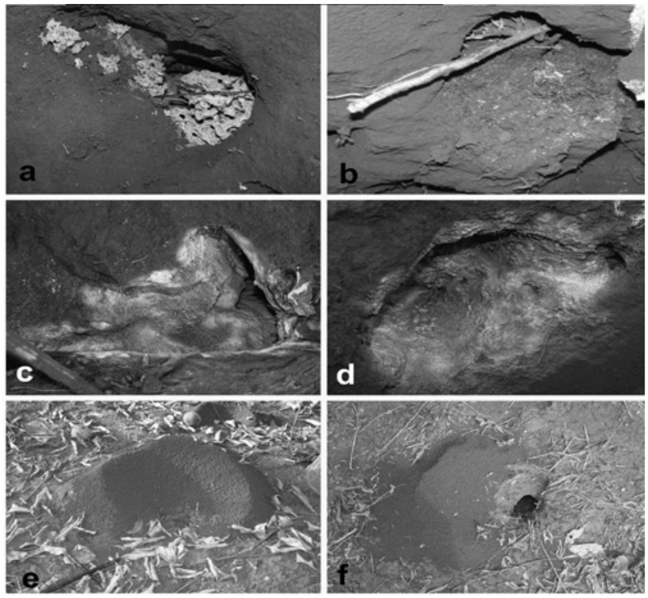

Figure 2. Nests of *Acromyrmex rugosus rugosus* marked with talcum powder. (**a**) Fungus chamber interwoven by roots. (**b**) Waste chamber. (**c**) Empty chamber. (**d**) Soil chamber. (**e**) Nest mound resembling a small crater in the form of a half-moon. (**f**) Irregular form of entrance hole.

their depths ($\chi^2 = 10.3$, d.f. = 3, p = 0.016), with fungus chambers being located closer to the surface (mean depth 34.4 cm, range 6–94 cm), while the deepest chambers contained waste material (mean depth 111 cm, range 7–250 cm; Fig. 3). Empty chambers and soil chambers were on average 64.6 cm (range 28–130 cm), and 76.2 cm (10–190 cm) in depth respectively (Fig. 3). Fungus gardens were on average 334.1 ± 218.9 (range 70–850 ml) in volume and were often much smaller than the chambers that contained them. The fungus was uniform in appearance and cultivated exclusively on the leaves of dicotyledonous plants (Fig. 2a), even in those colonies located in pasture. Waste chambers contained 1201.2 ± 1709.6 (range 50–5600 ml) of waste and soil chambers 1668.0 ± 2107.3 (range 40 to 4140 ml) of soil. Chambers were arranged at various angles relative to one another, varied widely in size and often had multiple, interconnected protuberances rather than being a smooth cavity (Fig. 1). Tunnels varied from 0.6 to 50 cm in width, were long or short, had no or many ramifications, and ran vertically, horizontally and along all inclines in between (Table 2; Fig. 1). Some chambers were connected to each other or entrance holes by several tunnels (Fig. 1e) and others by only a single tunnel (Fig. 1f), with the level of connection being independent of the size or shape of the chambers. Thus, the connections and arrangement of chambers and tunnels was irregular and followed no consistent pattern.

Myrmecophiles

As well as containing old fungus and ant body parts, waste chambers often also contained a great deal of soil. Many arthropods were found to be associated with the waste material: sowbugs (Crustacea, Isopoda), pseudo-scorpions (Arachnida, Pseudoscorpionida), collembolans, acarids, diplopods, chilopods, burrowing bug nymphs (Heteroptera, Cydnidae), beetle larvae (Coleoptera, Elateridae), beetle adults (Coleoptera, Scarabaeidae), and other coleopterans. The tunnels to some inactive waste chambers were blocked. Active waste chambers were always located beside or below the fungus chamber, but were always separated from it by tunnels.

Structural correlations

Of the four main nest attributes measured, three were closely related. The number of entrance holes was correlated with both the area of nest mound (rs = 0.80, p = 0.002) and the number of chambers (rs = 0.65, p = 0.023; Fig. 4). The area of nest mound and number

Table 1. Number and dimensions (mean, SD and range) of nest chambers, maximum depth of nest, area of the nest mound and number of entrance holes for *Acromyrmex rugosus rugosus* nests marked with talcum powder (1T to 8T) or cast with cement (9C to 12C).

Nest	Chambers (n)	Chamber length (cm)			Chamber height (cm)			Chamber width (cm)			Nest depth (m)	Nest area (m^2)	Entrance holes (n)
		Mean	SD	Range	Mean	SD	Range	Mean	SD	Range			
1T	2	48.0	31.1	26–70	11.0	2.8	9–13	8.0	1.4	7–9	0.09	0.03	1
2T	1	20.0	-	-	7.0	-	-	9.0	-	-	0.06	0.01	1
3T	2	65.0	7.1	60–70	12.0	2.8	10–14	7.5	0.7	7–8	0.10	2.66	5
4T	2	34.0	8.5	28–40	15.5	4.9	12–19	18.5	2.1	17–20	0.27	0.33	1
5T	8	28.4	14.3	12–50	15.8	3.7	10–20	17.4	5.8	11–28	2.50	0.26	5
6T	14	25.4	14.4	7–58	14.4	9.2	8–36	15.9	9.0	7–41	1.90	3.20	5
7T	10	25.2	11.6	13–43	12.6	4.4	6–20	16.6	8.2	6–34	1.70	1.00	4
8T	8	22.8	10.7	11–37	19.0	8.0	9–30	15.5	8.4	7–30	1.17	2.13	7
9C	9	22.6	8.8	8–38	12.4	4.0	7–20	15.7	6.6	7–26	3.75	2.65	5
10C	10	14.8	4.7	8–26	9.5	4.1	5.5–17	9.3	2.6	6–14	1.70	0.27	3
11C	18	19.9	11.6	6.3–46	12.5	7.0	3–33	13.8	7.2	5–28	1.74	4.08	6
12C	26	27.0	17.0	6.2–62	17.0	9.8	4–43	13.0	6.4	5–26	1.34	9.89	11

Table 2. Number and dimensions (mean, SD and range) of tunnels between each chamber or bifurcation for *Acromyrmex rugosus rugosus* nests cast with cement.

Nest	Tunnels (n)	Tunnel length (cm)			Tunnel height (cm)			Tunnel width (cm)		
		Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
9C	35	47.8	60.7	4.0–285.0	2.3	1.6	1.0–7.0	4.9	8.9	1.0–50.0
10C	42	23.6	18.4	1.0–85.0	2.1	1.2	1.0–6.0	3.4	2.0	0.9–7.0
11C	46	23.8	30.1	1.6–160.0	3.1	2.0	1.1–9.2	3.4	2.7	1.2–14.0
12C	84	26.9	23.3	1.5–108.0	2.8	1.6	1.0–8.0	3.4	2.5	0.6–14.5

of chambers was thus also related ($r_s = 0.73$, $p = 0.007$; Fig. 4). Depth, however, was not as clearly related to the other variables, being correlated only with the number of chambers ($r_s = 0.65$, $p = 0.023$; Fig. 4), and not with the number of entrance holes ($p = 0.150$) nor the area of the nest mound ($p = 0.216$).

Discussion

The nest casting techniques used provided new insights into the complexity of *Acromyrmex* nest architecture. Nest location was nonrandom, with nests normally being located in areas that made excavation difficult and which may thus provide some protection against predators such as armadillos (Rao, 2000). *A. rugosus rugosus* is evidently opportunistic when building nests and takes advantage of the immediate environment. This was most obvious when old roots of trees were utilized as 'guide-lines' for tunnels or chambers, most probably to reinforce the structural integrity of the nest. Previous studies have found *Acromyrmex* nests to be relatively small, with 14 being the maximum number of chambers recorded previously (Della Lucia and Moreira, 1993; Michels et al., 2001; Forti et al., 2006). While most of the *A. rugosus rugosus* nests examined in the current study were within this size range, several were noticeably larger than has previously been found, including one colony (12) with 26 chambers. The variation in the number of chambers most probably relates to the age of the colony and possibly seasonal changes (Lapointe et al., 1998; Moreira and Forti, 1999).

Chambers of *A. rugosus rugosus* were found from within a few cm of the surface to a maximum depth of almost 4 m. Almost all chambers, however, were less than 2 m deep while those of the smaller nests were less than 0.3 m deep. Although some species of *Acromyrmex* can also have deep nests, such as *A. landolti* (5 m depth) and *A. rugosus rochai* (4 m depth), most species have shallower nests up to 2 m deep and *A. rugosus rugosus* has only been recorded previously as having chambers up to 0.4 m deep (Gonçalves, 1961; Navarro and Jaffe, 1985). Humidity is critical to the growth of the mutualist fungus (Roces and Kleineidam, 2000), and we suggest that deeper nests may be constructed to utilize a soil humidity gradient that is better for the cultivation of the fungus. The fungus chambers themselves may be located closer to the surface to save the workers energy and time during the transport of substrates to the fungus chambers, since this can be considerable (Roces and Hölldobler, 1994;

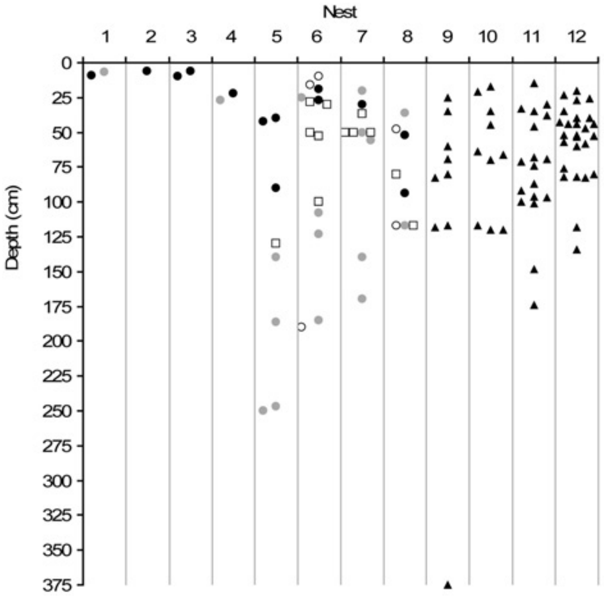

Figure 3. Depth of chambers found in the twelve *Acromyrmex rugosus rugosus* nests. For nests 1–8 which were marked with talcum powder, chambers are distinguished according to whether they contained fungus garden (black circles), waste material (grey circles), soil (open circles) or were empty (open squares). Chamber contents are unknown (black triangles) for nests 9–12 which were cast with cement. Within nests, chambers are offset horizontally solely for clarity and horizontal position therefore does not relate to actual horizontal position within the nest.

Denny et al., 2001). Variation between colonies may also relate to microclimatic conditions or differences in soil composition, with the maximum depth being limited by the water table (Jonkman, 1980).

The width of tunnels varied widely, even within the same nest. This variation may relate to the traffic of ants along them, as suggested previously by Moreira et al. (2004a). Unlike in *Atta* nests which generally have a series of main tunnels that connect to chambers via very short branches called peduncles (Jonkman, 1980; Moreira et al., 2004a,b; Andrade et al., 2005), the majority of tunnels in the *A. rugosus rugosus* nests connected directly to the chambers. Tunnels were also present in the nest mounds and were used by workers to transport leaves into, and soil out of, the nest. They may also have a role in ventilation, as is the case in *Atta vollenweideri* (Kleineidam and Roces, 2000).

One of the most interesting findings was the diversity of chambers found within the study nests. Previous studies have only recorded fungus chambers (Gonçalves, 1961; Della Lucia and Moreira, 1993; Forti et al., 2006), but our more thorough methods revealed the additional presence of chambers filled with soil or waste, as well as empty chambers. The latter are most probably prepared to receive fungus, waste or soil, and may thus be an indication that the nest is being expanded. Many species of *Acromyrmex* are known to incorporate rejected or exhausted fungal substrate in their nest mound, including *A. balzani, A. coronatus, A. fracticornis, A. hispidus, A.*

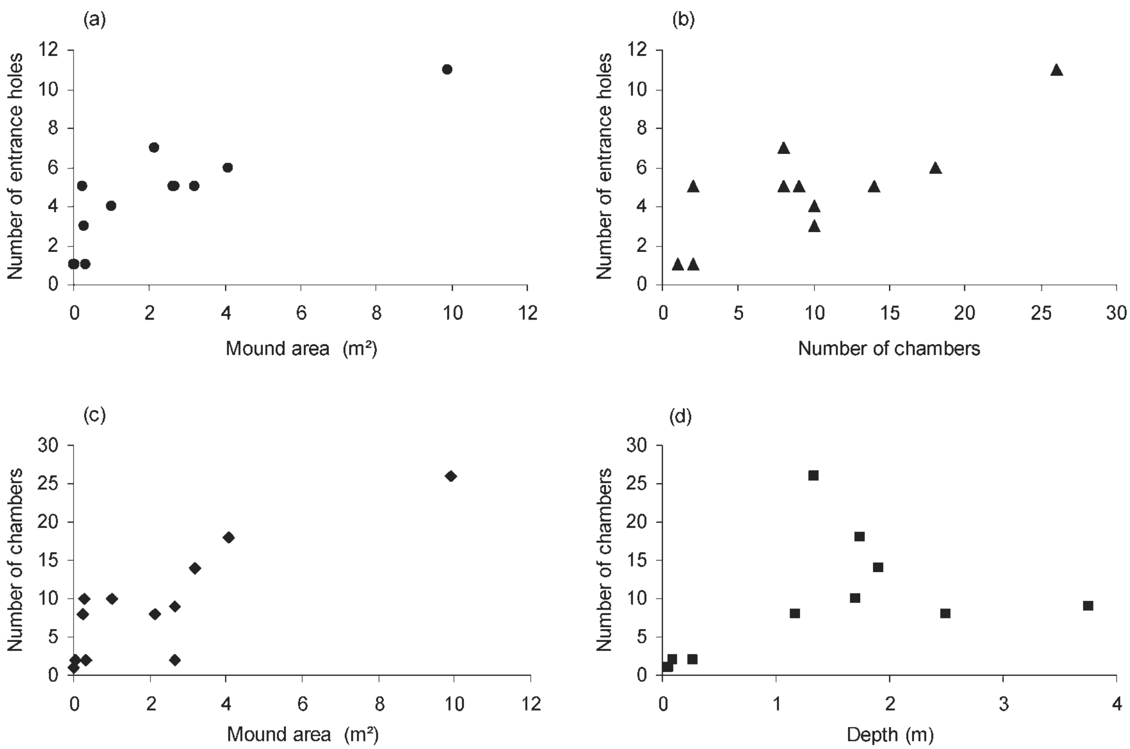

Figure 4. Relationships between the numbers of entrance holes or chambers, and the nest depths or mound areas, for the twelve *Acromyrmex rugosus rugosus* nests.

landolti, A. lobicornis, A. lundi pubences, A. striatus and *A. subterraneus* (Bonetto, 1959; Gonçalves, 1961; Zolessi and Abenante, 1973; Zolessi and González, 1974; Fowler, 1979, 1985; Pereira-da-Silva et al., 1981; Navarro and Jaffe, 1985; Mayhé-Nunes, 1991; Della Lucia and Moreira, 1993; Farji-Brener, 2000; Andrade, 2002; Forti et al., 2006). Lapointe et al. (1998) occasionally found chambers filled with exhausted leaf substrate in some nests of *A. landolti*, a grass-cutting species, but also observed that waste and excavated soil is normally disposed of externally by this species. In contrast to what is known for *Acromyrmex*, the majority of *Atta* species deposit waste material in internal waste chambers, with the exception of *Atta colombica* and *Atta mexicana* which deposit their waste externally (Haines, 1978; Deloya, 1988). Our study is therefore the first confirmation that at least one species of *Acromyrmex*, *A. rugosus rugosus*, also uses internal waste chambers for its waste material.

The waste chambers found in colonies of *A. rugosus rugosus* contained worker cadavers and arthropods of the same groups as found previously in *Atta* nests. The coexistence of inquilines in nests of leaf-cutting ants is very common because of the favorable temperature and humidity maintained inside the nests (Zolessi and Abenante, 1973; Zolessi and González, 1974; Della Lucia et al., 1993). These organisms can be specific to the host species (Farji-Brener and Sasal, 2003), but many, such as the Attini-beetle relationships (Navarrete-Heredia, 2001), are likely to be facultative. In addition to the macroorganisms identified, the waste material of leaf-cutting ant colonies will also include many microorganisms. These can include parasites of either the ants or their fungal mutualist, such as the fungi *Escovopsis*, *Metarhizium anisopliae* and *Aspergillus* (Bot et al., 2001; Hart and Ratnieks, 2001; Hughes and Boomsma, 2004; Hughes et al., 2004; Poulsen et al., 2006). Whether due to such pathogens or to direct toxicity, contact with waste material leads to increased mortality of workers (Bot et al., 2001). It seems likely that minimizing exposure to potentially pathogenic waste material is the reason why the tunnels to inactive waste chambers were generally found to be blocked in the nests of *A. rugosus rugosus.* The construction of internal chambers of waste and soil may perhaps be a strategy to reduce the exposure of workers to predators or parasites, such as phorid flies (Wetterer, 1995), when they are leaving the nest.

In conclusion, nests of *A. rugosus rugosus* are complex, often being large in depth, mound area, and number of chambers. They were discovered to contain a greater diversity of chambers than previously recorded, including chambers dedicated to waste material. The technique of marking or casting the internal structure of ant nests with substances such as talcum powder or cement is the best way of accurately mapping their subterranean architecture. It seems probable that the use of these techniques with other ant species may reveal their nests to also be more complex that currently realised.

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