RESEARCH ARTICLE

Nest structure engineering of the leaf-cutting ant, *Acromyrmex landolti*, in the semiarid Caatinga biome

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Abstract

Nest architecture is a key factor in the development of ant colonies. Species-specific constructed nests can be simple such as surface-level nests or elaborate such as subterranean or arboreal nests. Subterranean nests are more difficult to study and their internal structure is little known. This study was carried out with the objective of studying the structure of leaf-cutting ant nests in an extreme environment. For such, seven nests of *Acromyrmex landolti* were excavated in a semiarid region of the Caatinga, an exclusively Brazilian biome. The nests were measured both externally and internally and then photographed. Nests were found in open and sunny areas and externally all nests presented a loose soil mound, straw protection over the entrance hole, and a refuse dump. The number of underground chambers found ranged from 4 to 17, with differing heights, widths, and lengths. The chambers were found from near the surface of the ground to a maximum depth of 1.70 m. Our results showed that strategies used by *A. landolti* include the construction of an ornate straw tower at the entrance of the nest and the construction of deep underground rooms, with the chambers of fungi near the water table. The structure of the nests of *A. landolti* is probably related to its habit of building their nests in open, sunny locations associated with environmental factors characteristic of the semiarid climate of the Caatinga biome.

Keywords *Acromyrmex* · Behavioral strategies · Leafcutter ants · Nest architecture · Refuse disposal · Semiarid climate

Introduction

Most ants construct subterranean nests, built by excavating and moving a large amount of soil to the surface. The soil placed outside the nest facilitates their location and identification (Forti 1985) and also differentiates them from nests of other social insects that are constructed with materials such as paper, mud, or wax (Theraulaz et al. 1998; Tschinkel 2015). Subterranean nests are more difficult to study and vary in their internal complexity from shallow and simpler nests to those that reach 7 m deep and have numerous chambers of different shapes and functions connected by tunnels (Hölldobler and Wilson 1990; Moreira et al. 2004a). The main function of the structure of these subterranean nests, as well as that of surface, arboreal, and other social insect nests, is to protect the queen, offspring, and adults from natural enemies and other hazards. The nests also favor the production of appropriate microclimatic conditions for the maintenance of the colony (Sudd 1982) and, in the case of fungal cultivator species, for the cultivation of the symbiotic fungi (Kleineidam and Roces 2000; Bollazzi and Roces 2002; Verza et al. 2017).

It should be emphasized here that the energy spent in the construction of the nest cannot be recovered, unlike that spent in the production and care of eggs and larvae, which can serve as an alternative source of energy for adults in the event of food shortage. According to Mikheyev and Tschinkel (2004), if a colony changes nests twice a year, it would spend about 20% of its energy on building nests. Therefore, the internal and external architecture of ant nests should provide benefits that justify the high energy cost of their excavation.

Leafcutter ants belong to the genera *Atta* and *Acromyrmex* and are considered to be pests in agricultural and silvicultural areas of the Neotropics (Mariconi 1970), as they

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consume a greater amount of vegetation than any other local herbivore (Fowler et al. 1986; Hölldobler and Wilson 1990). The ants use these plants as a substrate for the fungi that they grow and feed, maintaining a symbiotic relationship (Weber 1972; Wilson 1980). Despite the designation of these ants as pest species, it is impossible to deny the benefits that they can bring from the construction of their nests. These include positive impacts on the chemical and physical properties of the soil that favor its fertility, which promotes the efficient cycling of nutrients and the growth of plants in many ecosystems (Coutinho 1982; Haines 1983; Moutinho et al. 2003).

Atta and *Acromyrmex* nests have very different structural characteristics (Hölldobler and Wilson 1990). It is worth highlighting here that nest architecture can be influenced by soil type, local climatic conditions, water table limit, and colony age (Jacoby 1950; Jonkman 1980; Moreira et al. 2004a). Mature nests of *Atta* may have more than 7000 subterranean chambers that are connected to each other and the surface via tunnels (Moreira et al. 2004a). In contrast, *Acromyrmex* have small nests, which usually contain only one or a few chambers (Gonçalves 1961, 1964; Fowler 1979). The maximum number of chambers previously reported for a nest of this genus was 26 (Verza et al. 2007). The exteriors of *Atta* nests are mainly characterized by one or several loose earthen mounds, formed by the accumulation of soil extracted from the chambers (Autuori 1942; Forti 1985; Moreira et al. 2004a, b), while in *Acromyrmex*, the mounds may not be present. Both have entry or exit holes for the foraging or removal of soil excavated by the workers (Gonçalves 1964; Della Lucia and Moreira 1993).

Leafcutter ants are highly specialized in nest construction. The genus *Acromyrmex*, for example, has nests that exhibit differences in both structure and shape, which may sometimes contribute to species identification (Gonçalves 1967; Pacheco and Berti-Filho 1987; Forti et al. 2006; Verza et al. 2007, 2017). Thus, while many species have a lot of loose soil around the entrance hole, including *A. rugosus* and *A. subterraneus*, it is known that *A. balzani*, *A. landolti*, and *A. fracticornis* build a straw tube over the nest entry hole. Underground nests reach a depth of almost 5 m, but most are shallow and reach a maximum of 60 cm (Gonçalves 1961; Fowler 1979; Farji-Brener 2000, Verza et al. 2007, 2017). The present study was performed with the objective of studying the external and internal architecture of the nests of *A. landolti* in a semiarid environment.

Materials and methods

This study was conducted in an irrigation area in the Caatinga biome, Petrolina-PE, at the Science Campus Agrarian (CCA) of the Federal University of São Francisco Valley-UNIVASF, located in the geographic coordinates: 9°19′10″S and 40°33′39″W, with an average altitude of 376 m. The predominant climate in the Caatinga is semiarid, an exclusively Brazilian biome. According to Sena (2011), the semiarid climate of this region has approximately 400 mm of precipitation per year. In this location, significant droughts occur, with strong winds and almost cloudless sky, high temperatures with average around 30 °C, and, according to Santos (2009), on some days, the temperature can exceed 45 °C and the soil temperature can reach 60 °C. A semiarid climate is one of the hottest and driest on the planet.

The soil of the study region is sandy, shallow, and stony and the drainage network of the area is very vast, consisting of large rivers. One such river is the São Francisco, considered the most important river in the region, because it allows irrigation along its banks. Among tree and shrub vegetation adapted to the dry climate, a predominance of species have stems with the capacity to store water such as cacti with thorns and very few leaves (Santos 2009).

Seven random *A. landolti* nests of differing external dimensions (length and width) were excavated in the months of August to October (dry season) of 2015. This ant was selected, because it is the most abundant leaf-cutting ant species in the area. The nests were all marked internally with cassava starch, which was introduced via one of the entrance holes using manual sprinkling equipment, to provide better visualization of the structure of the chambers and tunnels.

Before beginning the excavation, the nests were measured externally (the greatest width and length of the mounds) and photographed. An average distance of 10 m between nests was adopted. The excavation process then proceeded, following the methods of Verza et al. (2007, 2017), by carefully opening a small ditch around the nesting area, excavating from the inside out and digging deeper in accordance with the appearance of the chambers; attention was directed toward the tunnels with the aim of not losing any chambers. The chambers were quantified and the following measurements were taken: nest depth in relation to the ground level and the length, width, and height of the chambers. To determine the contents of the fungal chambers, the entire fungal culture of each chamber was placed in acrylic pots and taken to a laboratory, where its total volume was measured using 2 L graduated cylinders.

Data analysis

Using the recorded measurements, the average, standard deviation, and maximum and minimum range of the chambers and tunnels were calculated. The average and standard error of the depth (cm) of the chambers with different contents were also calculated. To verify correlations between the external area (m²), number of holes, number of chambers, and maximum depth (m), the Spearman correlation

coefficient was used at a 5% significance level. The software used to conduct the analysis was the Bioestat, version 5.3.

Results

It was verified that the nests of the leafcutter ant *A. landolti* externally present only one loose, circular earthen mound, with one or two entrance holes. Generally, one or more

bifurcated grass tubes were present in one of the holes, forming a tower and connected to each other in a single entrance hole (Fig. 2a, b). The height of the towers was 2.3–20 cm, while the average diameter was 1.0 ± 0.4 cm. The largest nest had an external area of 1.20 m^2, while the smallest had an external area of 0.20 m^2 (Table 1).

All nests exhibited waste deposition outside the nest. Deposition of waste and soil in the external area of the nest occurs through the formation of small mounds, usually with

Fig. 1 Depth of the chambers found in the seven *Acromyrmex landolti* nests examined in this study. Nests are numbered from 1 to 7, the chambers are categorized by their contents: fungal gardens (black circles), soil with dry fungus (gray circles), empty (open circles), or soil (open squares)
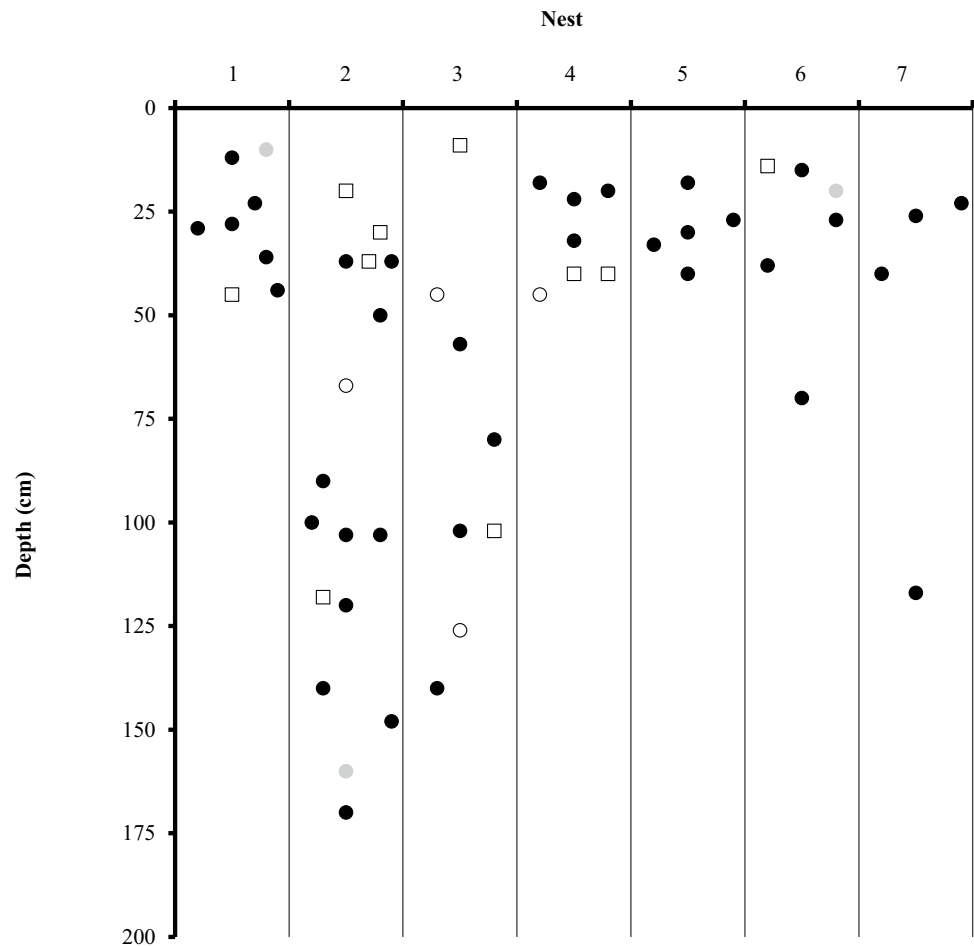
Table 1 Number and dimensions (average, standard deviation (SD), and amplitude) of the chambers, maximum depth, external area, and number of entrance holes of *Acromyrmex landolti* nests

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	8	12.0	2.4	7–14	8.1	2.5	5–12	8.9	3.2	2–13	0.45	0.40	1
2T	17	19.1	8.2	10–40	11.6	5.2	7–30	11.1	2.7	6–19	1.70	1.20	1
3T	7	15.6	4.7	9–20	8.6	1.5	7–10	10.7	2.6	8–14	1.40	0.56	1
4T	7	8.1	2.4	5–12	7.0	1.4	5–9	6.9	2.5	5–12	0.45	0.65	2
5T	5	8.2	1.3	7–10	7.4	1.9	5–10	7.4	1.8	5–10	0.40	0.49	1
6T	6	10.5	2.2	8–14	6.5	1.5	5–9	8.0	1.8	6–10	0.70	0.20	1
7T	4	17.0	5.4	5–17	9.0	2.5	3–9	13.0	3.9	4–13	1.17	0.23	1

refuse dumped on or beside the soil mound (loose, compact, and/or granulate) and at a distance of approximately 10 cm from the entrance hole (Fig. 2a).

Most of the chambers examined contained fungi (Fig. 1). In addition to fungal chambers, nests 1, 2, 3, 4, and 6 contained chambers with soil, empty chambers, and chambers with soil and aged dry fungus (Fig. 1) separated by bifurcated tunnels that connected two or more functionally independent chambers. Across all nests, 4–17 irregularly shaped chambers were found in each nest (Table 1, Fig. 1). Chambers were distributed irregularly; however, they were almost always below the tower region and loose earthen mounds or in that vicinity. Some arthropods were found inside the nests; the most abundant were pseudoscorpion, larvae of Elateridae, and other adult beetles.

The volume of fungal cultures ranged from 68 to 650 mL, often with the fungal garden small in relation to the size of the chamber (Fig. 2c). The fungal cultures exhibited a uniform appearance and were cultivated exclusively on leaves of monocotyledons. The heights (5–30 cm), widths (2–19 cm), and lengths (5–40 cm) of the chambers were variable, exhibiting differences within nests; chambers were sometimes impossible to measure due to their irregular shape (Table 1).

The chambers were found from near the surface (9 cm) to a maximum depth of 1.70 m (Table 1, Fig. 1), being limited by the water table (Fig. 2d). The highest frequency of chambers occurred at a depth of up to 40 cm from the surface, with more than 50% of the chambers containing fungi, offspring, and ants; empty chambers only occurred at a depth of up to 40 cm (Fig. 1).

There was no correlation between number of holes and the external area (mounds of waste and soil) of the nest ($rs = -0.17$, $p = 0.7210$), the number of chambers ($rs = 0.10$, $p = 0.8261$), or the depth ($rs = 0.35$, $p = 0.4366$). The number of chambers also did not correlate with the external area ($rs = 0.61$, $p = 0.1391$) or depth ($rs = 0.07$, $p = 0.8767$), however, a decrease in the number of chambers with increasing depth was observed in the nests with larger chambers. There was no significant correlation between the nest's depth and the size of the external area ($rs = 0.47$, $p = 0.2855$).

Fig. 2 *Acromyrmex landolti* nests: **a** detail of the entrance tube and mound, **b** entrance tower with several interconnected tubes, **c** chamber with symbiotic fungus, offspring, and workers, and **d** depth limited by the water table

Discussion

This investigation showed that leafcutter ants (*Acromyrmex landolti*) found in the semiarid Caatinga biome (hot and dry weather) have deep nests that differ from the nests of the same species studied by Rodrigues (not published dissertation 2012) in the pastures of southwest Bahia with humid climate, which had a maximum depth of 78.0 cm. In the present study, depths of nests were limited by the water table and channels or deep chambers containing fungi were usually very close to the water or submerged in it. The excavation period was during a warm and dry season with strong winds and an almost cloudless sky. Therefore, the deeper nests may have been constructed to use the soil moisture gradient to achieve the appropriate conditions for the cultivation of the symbiotic fungus.

During the excavations, a relatively large number of chambers were found: only one nest had 17 chambers, the highest number recorded in this study. Rodrigues (unpublished dissertation 2012) found from 1 to 11 chambers per nest for the same species. In relation to the number of chambers in nests of other grass cutting ants such as *Acromyrmex balzani*, Silva et al. (2010), Caldato et al. (2016), and Verza et al. (2017) found a variation between 1 and 14 chambers per nest.

In this study, no refuse chambers were found and all nests were observed to have refuse dumps in their external area. However, in addition to the already-reported fungal chambers (Gonçalves 1961; Della Lucia and Moreira 1993; Forti et al. 2006), chambers storing excavated soil were found. The presence of these chambers is different from nests of *A. balzani*, where no such soil chambers were observed and the excavated soil was placed in the refuse chambers and in the external area of the colony (Verza et al. 2017). Empty chambers, which were probably reserved for fungi or soil, were also found. According to Specht et al. (1994), each species has behaviors and needs that are linked to the environment in which they live.

In addition, chambers containing soil with dry fungus and several live ants were also found. In one nest, a chamber with these contents also had dead ants, but did not look like a refuse chamber. Perhaps these chambers are temporary refuse dumps or transport chambers, as occur in some species of ants such as *Pogonomyrmex badius* (Tschinkel et al. 2015) and *Acromyrmex lundii* (Römer et al. 2018), which move seeds, garbage, and soil up and down in a series of steps. Additionally, it was only 10 cm deep and refuse chambers are usually found in *Acromyrmex* nests at depths greater than 20 cm. Lapointe et al. (1998) occasionally found chambers filled with exhausted leaf substrate in some *A. landolti* nests. The same authors also mention that the workers of this species usually carry the refuse and the soil excavated to the surface, where these materials form characteristic mounds near the entrance of the colony.

According to several studies, many species of *Acromyrmex* build an external earthen mound, often interspersed with vegetal material, but this cannot necessarily be considered as refuse (Bonetto 1959; Gonçalves 1961; Fowler 1985; Forti et al. 2006). The species of *Acromyrmex* that effectively dispose of their refuse externally are *A. coronatus*, *A. fracticornis*, *A. hispidus*, *A. landolti*, *A. lobicornis*, *A. lundii pubences*, *A. striatus*, and *A. subterraneus* (Bonetto 1959; Gonçalves 1961; Zolessi and Abenante 1973; Zolessi and González 1974; Fowler 1979; Navarro and Jaffe 1985; Pereira-da-Silva et al. 1981; Della Lucia and Moreira 1993; Farji-Brener 2000; Forti et al. 2006). While *A. balzani* and *A. rugosus rugosus* deposit refuse externally and in internal chambers, refuse chambers are found in deeper nests (Verza et al. 2007, 2017).

Most species of *Atta* deposited discharged material particles that had been used in the cultivation of the fungi in internal refuse chambers. *Atta colombica* and *Atta mexicana* are exceptions and deposit refuse externally (Haines 1978; Deloya 1988). This species distributes its chambers irregularly, almost always immediately beneath the earthen mounds or very close to them. The determination of the location of the highest concentration of chambers is a relevant factor that is critical for pest species control decisions (Moreira et al. 2004a). Although there was no correlation between the number of chambers and depth, it was observed in the colonies with the largest number of chambers that this number reduced with increasing depth. In this study, most chambers were observed at a depth of up to 40 cm from the surface, with more than half being fungal chambers. Empty chambers were present only from 40 cm deep. Our findings were similar to that of Rodrigues (2012) who observed that more than 50% of the chambers up to 45 cm deep in *A. landolti* nests were occupied by fungi and empty chambers were present only from this depth.

The differences in chamber dimensions observed in *A. landolti* nests are common in ant nests such as those of *A. rugosus rugosus*, *Atta vollenweideri*, *P. badius*, *Formica pallidefulva*, *Camponotus socius*, *Atta bisphaerica*, and *A. laevigata* (Jonkman 1980; Tschinkel 2003, 2005; Moreira et al. 2004a, b; Verza et al. 2007). These variations in size can be considered adaptive specializations (Mikheyev and Tschinkel 2004) or may be due to the requirement that nest increases in size to accommodate the increase in the number of workers. It is important to emphasize that the workers exhibit opportunistic behavior in relation to the place where they build their nests, because unoccupied holes are often used as chambers. According to Wilson (1975), the construction of ant nests is related to the ecology and behavior of the species, which is related to their development and specialization. Therefore, species-specific nest characteristics

are common; however, there are elements that occur in most or all ant nests such as the tunnel-connected chambers (Tschinkel 2003, 2004).

During the excavations, several arthropods were found to be associated with *A. landolti* nests. The coexistence of tenants in the nests of leafcutter ants is very common due to the favorable conditions of temperature and humidity (Zolessi and Abenante 1973; Zolessi and González 1974; Della Lucia et al. 1993; Verza et al. 2007, 2017). However, it is not known how these myrmecophiles interact with the host ants in question.

In most of the nests of this species, holes were used by the workers to transport leaves into the nest and to bring soil and refuse to the surface. In *Atta vollenweideri*, these holes may also be used to regulate the ventilation of the nests. According to Kleineidam et al. (2001), wind is essential for respiration by these ants and their symbiotic fungi.

During this study, all nests were found in open and sunny areas. Although some nests were found in areas dominated by dicotyledonous plants, the fungi were cultivated using monocotyledon leaves, as was also observed by Gonçalves (1961). In this study, it was observed that this species sometimes travels several meters via chemical tracks until an attractive substrate is found. In the studied biome, beside *A. landolti* nests, *A. rugosus rugosus* and *A. balzani* nests, dicotyledonous and monocotyledon leafcutters, respectively (Verza et al. 2017), were also identified, but these last two species were found only in shaded places.

In general, *A. landolti* nests are deep and complex for this genus. The chambers are irregularly shaped and are interconnected through underground tunnels. Although there are chambers with several functions such as containing aged fungus, no refuse chambers were found and refuse was instead found in deposits outside the nest. Furthermore, the nests of these ants often possess a tower around the entrance hole formed by a straw tube or, surprisingly, were sometimes ornamented with several interconnected tubes that connect the external environment to the subterranean environment. In addition to the nests of *A. landolti*, the nests of *A. balzani* and *A. fracticornis (*monocotyledon leafcutters) found in different biomes also feature a straw tube guiding to the entrance hole, but only one tube (Gonçalves 1961; Forti et al. 2006; Verza et al. 2017), unlike the nests of *A. landolti* found in Caatinga, which feature an ornate straw tower with two or more than ten tubes above the entrance hole. It is believed that these structures are a strategy to protect the entrance of the nest from environmental events characteristic of the semiarid climate of the Caatinga biome that would be unfavorable for the survival of the ants. This strategy may allow them to build their nests in open spaces.

Additionally, it appears likely that the nest depths of this species may be related to their microclimatic requirements, since the fungal chambers containing the offspring were the deepest and limited by the water table. This adaptive occurrence of behavioral patterns is probably due to the high temperatures and low soil moisture characteristic of the semiarid Pernambuco region. These structures probably serve to regulate the humidity and temperature of the colony and to maintain the appropriate conditions for the cultivation of the symbiotic fungus. In the semiarid region of the Caatinga Bioma, the nests of these social insects are elaborate fortresses.

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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