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Original Article

The nest architecture of the leaf-cutting ant *Atta sexdens* (Hymenoptera: Formicidae)

A arquitetura do ninho da formiga cortadeira *Atta sexdens* (Hymenoptera: Formicidae)

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Abstract

Nests of species of the genus *Atta* are, structurally, the most complex among those of the Attini tribe. The objective of this research was to describe external and internal characteristics of nests of the leaf-cutting ant *Atta sexdens* (L. 1758) (Hymenoptera: Formicidae) in Vitória da Conquista, Bahia state, Brazil. Ten nests (N1 to N10) of this ant were selected and their external architecture described according to the loose soil removed from excavations by ant forage workers. The length and width of foraging trails and the distance of their entrance holes to the mound of loose soil in nests of this ant were measured. The internal architecture and the number, shape, dimensions and depth of the internal chambers and tunnels of the N1, N2 and N3 nests, with loose soil areas of 78.02, 8.06 and 4.78 m2, respectively, were described and measured. The nest N1 was excavated without moulding and the N2 and N3 moulded with 5 kg of cement in 10 L of water and subsequently excavated. Trenches, one meter deep, were made before excavation began and widened and deepened until exposing the chambers and tunnels of these nests. The ants deposited loose soil irregularly, forming small mounds around the entrance holes of their nests. Fungus and empty chambers are spherical with twig-like branches. The inner sections of the tunnels are elliptical or circular with different dimensions.

Keywords: external and internal architecture, foraging tunnels, sauvas.

Resumo

Os ninhos das espécies do gênero *Atta* são, estruturalmente, os mais complexos entre aqueles da tribo Attini. O objetivo desta pesquisa foi descrever as características externas e internas de ninhos da formiga cortadeira *Atta sexdens* (L. 1758) (Hymenoptera: Formicidae) em Vitória da Conquista, estado da Bahia, Brasil. Dez ninhos (N1 a N10) dessa formiga foram selecionados, e sua arquitetura externa descrita de acordo com a presença de solo solto removido pelas operárias forrageiras durante as escavações. O comprimento e a largura das trilhas de forrageamento e a distância dos orifícios de entrada até o monte de solo solto nos ninhos dessa formiga, foram medidos. A arquitetura interna, incluindo o número, formato, dimensões e profundidade das câmaras e túneis internos dos ninhos N1, N2 e N3, com áreas de solo solto de 78,02; 8,06 e 4,78 m^2, respectivamente, foi descrita e mensurada. O ninho N1 foi escavado sem moldagem e os N2 e N3 moldados com 5 kg de cimento em 10 L de água e escavados. Trincheiras de um metro de profundidade foram feitas antes do início da escavação e, posteriormente, alargadas e aprofundadas até a exposição das câmaras e túneis desses ninhos. As formigas depositaram o solo solto de maneira irregular, formando pequenos montes ao redor dos orifícios de entrada de seus ninhos. As câmaras de fungo e as vazias são esféricas com ramificações semelhantes a galhos. As seções internas dos túneis, de ninhos dessa formiga, são elípticas ou circulares e com diferentes dimensões.

Palavras chaves: arquitetura externa e interna, túneis de forrageamento, sauvas.

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1. Introduction

The leaf-cutting ants perform important ecological functions (Santos and Sousa-Souto, 2021; Lutinski et al., 2023; Oliveira et al, 2024), including soil aeration, seed dispersal, and nutrient cycling in ecosystems (Nascimento et al., 2024). *Atta sexdens* (L. 1758) (Hymenoptera: Formicidae) stands out for its large nests and complex social organization. The morphological traits of its workers and the characteristic loose soil mounds deposited over mature nests facilitate its identification in natural environments (Mariconi and Zamith, 1963; Mariconi, 1970). Understanding the nesting architecture of this species can provide insights into its biology and ecological role within forest ecosystems.

Species of the genera *Atta*, *Acromyrmex* and *Amoimyrmex* (Hymenoptera: Formicidae) (Cristiano et al., 2020) build large and elaborated nests which, combined with their social organization, enhance protection against predators, parasitoids, and pathogens (Britto et al., 2016). Nests of ants and other social insects protect the offspring and the queen against natural enemies, facilitating food distribution and control of the microclimate (Sousa et al., 2022 a, b).

Excavated soil over their surface and tunnels, besides the interior with interconnected chambers and galleries characterize nests of leaf-cutting ant nests. The ants move through tunnels of varying diameters and shapes connecting the chambers to tunnels in the loose soil mounds. Foraging tunnel entrances, located at varying distances from the loose soil area, are used to transport cut leaves into the nest and are important for air circulation and gas regulation, facilitating carbon dioxide release helping to maintain the internal environmental conditions adequate for the colony development and survival (Forti et al., 2017). This more integrated view of tunnel functions aligns with recent studies highlighting the complexity of the foraging system and nest dynamics (Lopes et al., 2016; Caldato et al., 2020) emphasizing the importance of foraging networks for colony organization and efficiency.

The shape, location, and dimensions of internal chambers in *Atta* nests depend on the species and the function of each chamber—such as fungus-growing, refuse, empty, or filled with loose soil (Mariconi, 1970). Excavation studies contributed to understanding of the biology of leaf-cutting ants and the development and refinement of control strategies (Moreira et al., 2004a, b). The process of moulding in cement allows observing tunnel types in *Atta* nests, including thin ones for communication between the larger ones with a circular section, more or less perpendicular, with 3 to 4 cm in diameter, and those with an elliptical section, generally horizontally, 10 to 12 cm in diameter (Jacoby, 1950). The tunnels, in the nests of *A. sexdens*, can be circular with a diameter of 2.4 to 4.0 cm, where the ants move from the inside to the outside of their nests (1); elliptical about 1.5 cm high and 5 cm wide, where soldiers pass (2); with 2 cm in diameter connecting the chambers to the ventilation places (3); and radially up to 200 m long from the nest to plants foraged (4) (Eidmann, 1932). The movement of ants in tunnels, with elliptical and circular sections, is similar (Jacoby, 1950) the understanding of these structures, including their role in gas exchange increased with studies (Sousa et al., 2021; Sousa et al., 2023) on microenvironmental preferences for nest founding (Sousa et al., 2022c), and behavior of founding queens (Mota-Filho et al., 2021). In addition, the dynamic construction and expansion of grass-cutting ant nests of *Atta bisphaerica* Forel, 1908 (Hymenoptera: Forimicidae) and *Atta capiguara* Gonçalves, 1944 (Hymenoptera: Forimicidae) were sudied (Farias et al., 2020).

The objective of this research was to describe external and internal characteristics of nests of the leaf-cutting ant *A. sexdens* in Vitória da Conquista, Bahia State, Brazil.

2. Material and Methods

Ten *A. sexdens* nests were marked in Vitória da Conquista, Bahia State, Brazil. The external architecture of these nests was determined by measuring the greatest length and width of loose soil above each ant nest. The mounds of loose soil were measured and two nylon ropes extended over each nest forming an orthogonal axis (x, y) to help locating the holes in relation to the nest centre. The number and diameter of exit holes of *A. sexdens* tunnels were determined.

Baits made with plastic straws (Moreira et al., 2004a, b), cut into 4 mm and separated by colour, were placed in a solution of orange juice and sugar, drained and transferred to trays with dehydrated citrus pulp and ground. This mixture was dried in the sun for 48 hours and placed in plastic bags, separated per colour and placed near the holes marked and its colour recorded. After 24 hours, the colour of the straw returned by the ants above each nest was observed to assess the number of holes per *A. sexdens* nest. The distance, length and width of the foraging trails were measured in relation to the mound of loose soil per ant nest.

The external and internal architecture of the nests N1, N2 and N3 was studied using partial (N1) and total (N2 and N3) excavation processes, with and without cement moulding. The nest N1 was partially excavated without moulding and the N2 and N3 moulded using a mixture of 5 kg of cement for 10 L of water (Moreira et al., 2004a) to facilitate the visualization of the shape and distribution of its chambers and tunnels. The excavation of the nests N2 and N3 started 48 hours after its moulding with cement by opening a trench 1 m deep, just before the beginning of the loose soil above them until reaching their chambers and tunnels. These excavations continued until exposing all chambers, which were numbered and their depth in relation to the ground and the height, length and width of each tunnel measured. The height, width, length and depth of some tunnels external to the nest, in relation to ground level and the chambers and tunnels below the area with loose soil for the N3 nest were measured.

3. Results

The average area of loose soil, number and diameter of holes connected to the tunnels and the diameter of the holes in the loose soil area in the ten *A. sexdens* nests ranged from 17.63 to 260.80 m^2, 15 to 74 and 1.3 to 12.5 cm, and 3,1 a 5,7 cm respectively (Figure 1, Table 1).

The shape of the tunnels in the nests N1 and N2 were elliptical or circular with a maximum and minimum width and height of 28.0 and 3.0 cm and 9.0 and 1.5 cm, respectively (Table 2).

The average width, height and length of the chambers with fungus of the nests N1, N2 and N3, were 22.6, 18.4 and

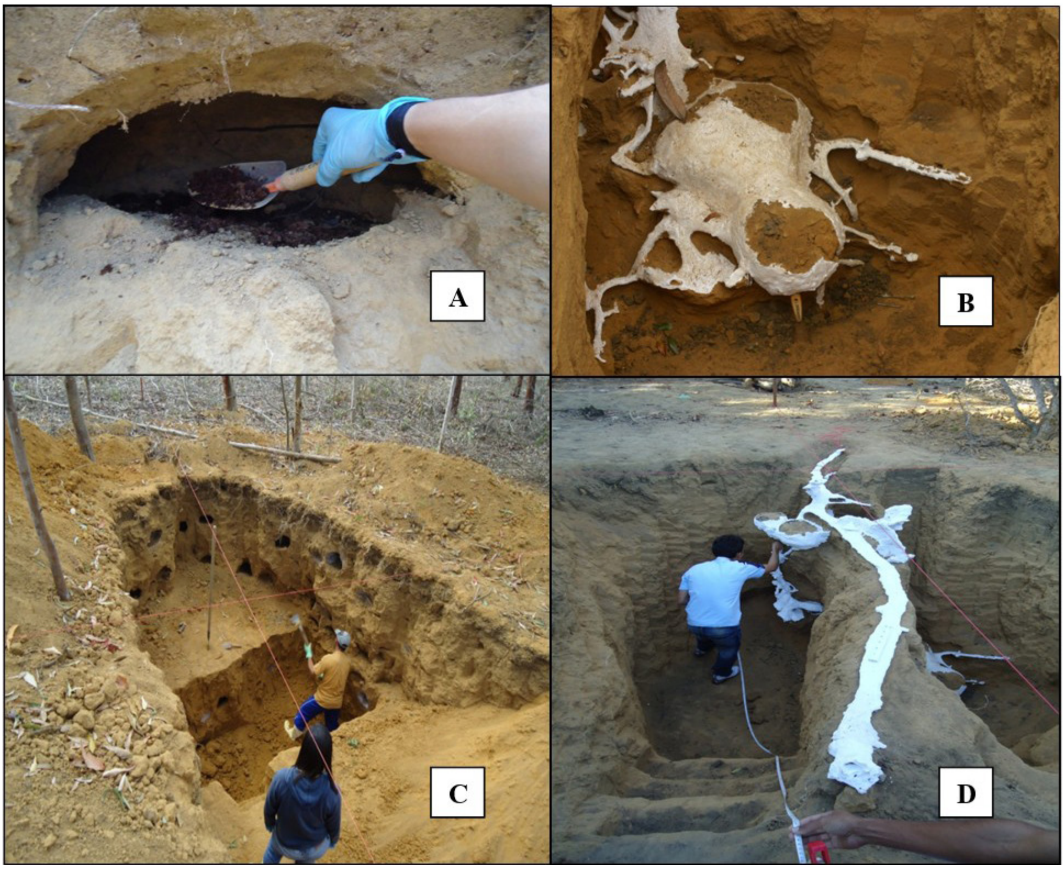

Figure 1. Excavation of the *Atta sexdens* (Hymenoptera: Formicidae) nest: A – garbage chamber of the nest N1; B – garbage chamber of nest N2; C – nest N1, and D – nest N2.

Table 1. Length (L), width (W) and area (A) of loose soil, number of holes on the main loose soil mound (NHMLS), number of smaller mounds (NSM) and maximum (Max.), minimal (Min.) and mean (Me.) of diameter of holes on the loose soil mound (DASL) per *Atta sexdens* (Hymenoptera: Formicidae) nest in Vitória da Conquista, Bahia state, Brazil.

Nest	L (m)	W (m)	A (m²)	NHMLS	NSM	DASL (cm)		
						Max	Min	Me
N1	3.7	6.4	23.68	31	11	4.6	1.5	3.1
N2	6.3	6.7	42.21	22	06	6.0	2.5	3.8
N3	4.2	2.9	24.36	18	05	6.0	3.0	4.3
N4	7.4	3.0	22.20	15	09	9.0	3.0	5.5
N5	16.0	16.3	260.80	74	34	12.5	1.3	4.7
N6	5.0	6.3	31.50	30	07	6.0	1.5	3.6
N7	8.2	6.3	51.66	44	08	9.0	3.0	5.7
N8	7.0	5.2	36.40	42	07	9.0	2.3	4.9
N9	17.0	7.0	119.00	69	20	6.8	2.5	4.1
N10	4.3	4.1	17.63	20	04	6.8	3.0	4.4

18.4 cm, 17.4, 15.4 and 9.1 cm and 24,2 and 21.3 and 19.7 cm and those with garbage of 23.7 and 34.0 cm, 17.7 and 30.0 cm and 39.6 and 43.0 cm in the nests N1 and N2, respectively (Table 3).

The numbers of chambers in the nests N1, N2 and N3 of *A. sexdens* were 182, nine and seven, respectively, with 43 chambers with fungus, 114 empty and 25 with garbage in the N1 nest. Nine chambers, eight with fungus and one possibly with garbage, whose content was not determined because it was moulded with cement, were found in the nest N2 and seven chambers with fungus in the N3 (Table 3).

The chambers of the *A. sexdens* nests were spherical, except for the garbage ones, ellipsoidal and with extensions similar to twigs and larger and deeper than the others.

4. Discussion

The area of loose soil and the number and diameter of holes vary between species and genera of leaf-cutting ants, such as those of *Acromyrmex rugosus rugosus* Smith, 1858 (Hymenoptera: Formicidae) with an area of loose soil from 0.01 to 9.89 m^2 and with one to 11 entry holes, most of which near the loose soil mounds (Verza et al., 2007).

The elliptical or circular shape of the tunnels of the N1 and N2 nests of *A. sexdens* is due to their function (Jacoby, 1950). The elliptical tunnels, being wider, allow the passage of a greater number of workers carrying leaf fragments from the outside to the inside of the nest and, similar to the chambers, may be hypothetically enlarged through a self-organized process resulting from worker

Table 2. Smallest (S), largest (L) and mean (M) values of the width (W), length (L), total length (TL) and depth at the ground level (Depth) of the tunnels of the nest N3 of *Atta sexdens* (Hymenoptera: Fomicidae). Vitoria da Conquista, Bahia state, Brazil.

Tunnel	Width (cm)			Height (cm)			TL	Depth (cm)		
	S	L	M	S	W	L		S	L	M
01	5.2	7.9	6.4	4.0	5.1	4.7	65.0	38.0	211.2	124.9
02	3.8	6.7	5.2	1.9	2.9	2.3	206.4	134.5	154.2	144.6
03	7.1	10.9	9.0	3.1	6.3	4.4	36.2	104.8	107.0	106.0
04	1.7	2.1	1.9	1.6	2.3	2.0	21.2	105.2	105.5	105.4
05	3.9	6.8	5.2	2.2	5.0	3.3	164.1	33.5	41.6	38.1
06	4.2	6.4	5.2	2.1	3.6	2.7	155.2	42.4	45.8	44.0
07	3.8	4.1	4.0	2.0	2.7	2.3	76.1	31.0	35.4	32.8
08	3.0	3.8	3.4	1.6	2.3	2.0	186.8	28.6	38.1	34.4
09	9.6	21.8	14.5	2.9	4.2	3.7	130.0	28.8	43.6	38.2
10	7.6	11.8	10.1	2.5	3.4	3.0	232.2	62.5	167.6	126.6
11	5.2	9.4	6.7	2.0	6.1	3.7	129.5	112.7	135.8	124.8
12	4.9	10.0	6.9	2.5	3.2	2.9	127.2	36.0	39.1	37.3
13	2.4	3.3	3.0	1.9	2.1	2.0	156.4	24.6	34.5	30.5
14	4.0	7.8	5.5	2.0	3.1	2.5	212.5	24.6	29.8	27.3

Table 3. Loose soil area (LA), type (CT) and mean width (W), height (H), length (L) and depth (DAL) in centimeters and total number of nest chambers (TNC) of the N1, N2, and N3 nests of *Atta sexdens* (Hymenoptera: Formicidae) in Vitória da Conquista, Bahia, Brazil.

Nest	LA (m²)	CT	W	H	L	DAL	TNC
N1	78.02	Fungus	22.6	17.4	24.2	104.6	43
		Empty	18.5	14.0	20.7	111.0	182
		Waste	23.7	17.7	39.6	96.4	25
N2	8.06	Fungus*	18.4	15.4	21.3	88.5	8
		Waste*	34.0	30.0	43.0	153.0	9
N3	4.78	Fungus	18.4	9.1	19.7	82.1	7

aggregation and density-dependent digging behavior around the relocated brood and fungus (Römer and Roces, 2014). On the other hand, circular tunnels are used for communication between the larger ones with a diameter and a circular section with three to 4 cm and more or less perpendicular compared to the others, generally horizontally, from 10 to 12 cm (Jacoby, 1950). The function of the tunnels descending towards the water table aims to obtaining this resource as observed for A. *sexdens* nests in the field (Jacoby 1950). The movement of smoke puffs, injected into holes above the nest, revealed a ventilation system in the *Atta vollenweideri* Forel, 1893 (Hymenoptera: Formicidae) nests (Jonkman, 1978, 1980). Individuals of this ant access their chambers through tubular galleries with a diameter of five to 8 cm (Jonkman, 1978, 1980).

The section of the supply tunnels of *Atta sexdens rubropilosa* Forel (Hymenoptera: Formicidae) differed from those of *Atta laevigata* F. Smith (Hymenoptera: Formicidae), moulded with cement, elliptical in some sections, with an average width and height of 14.12 cm and 2 cm and maximum and minimum of 24 and 3 cm and 9.5 and 1 cm, respectively. Besides, interconnected supply holes, arriving in a single tunnel directed to the area with the highest concentration of chambers, at an average depth of 55 cm, a maximum of 73 cm and a minimum of 27 cm was observed for this last ant (Moreira et al., 2004a). The tunnel depth increased as they approached the nest area, sometimes up to 1.20 m deep for *A. sexdens* tunnels (Pretto, 1996).

The width, height and average length of chambers of *A. sexdens* with fungus were similar to those of this ant in eucalypt plantations (Pretto, 1996), but chambers with larger diameters, between 20 and 40 cm long, have been reported for *Atta sexdens* (Mariconi and Paiva Castro, 1960) and smaller or medium for *A. capiguara*, approximately 21 cm high by 27 cm, 15 cm and 17 cm wide and from 17 cm and 16 cm long, respectively (Gonçalves, 1967) confirming differences in the dimensions of chambers of nests between *Atta* species.

Variations in the number of chambers in the nests N1, N2 and N3 of *A. sexdens* are common due to factors such as age and soil type (Farias et al., 2020; Nascimento et al., 2024). A plausible hypothesis to explain the differences observed among the nests of *Atta sexdens* is the interaction between nest age and variation in soil matrix, factors that may promote changes in the internal morphology of the nest. It is assumed that, in the early stages, nests develop vertically, deepening into the soil, and that, at a later stage, they expand horizontally due to the need for more space caused by the colony's population growth, as well as the expansion of the fungus garden cultivation (Farias et al., 2020; Nascimento et al., 2024). Four *A. sexdens* nests, excavated in a degraded pasture area in Botucatu, São Paulo state, Brazil had 1.75, 2.43, 2.66 and 4.17 chambers/m^3 and a total of 373 chambers, of which 344 with fungus (Pretto, 1996) and *A. cephalotes* nests had 1,027 chambers with 8.52 chambers/m^3 (Autuori, 1942).

The variation among species (interspecific) and within a single species (intraspecific) occurs due to the interaction between the stimuli from the excavating workers and the soil matrix in which they are located (Nascimento et al., 2024). It can be hypothesized that abiotic (e.g., soil type) and biotic (e.g., workers, fungus garden, brood, etc.) environmental stimuli are sufficient to trigger the excavation of a new nest chamber in a suitable location (Fröhle, 2009). For instance, under controlled laboratory conditions, leaf-cutting ant workers excavated chambers as soon as they were allowed to relocate the symbiotic fungus within an excavation arena, and the digging activity concentrated around the deposited fungus (Römer and Roces, 2014). This suggests that both abiotic and biotic stimuli are necessary for the formation of a nest chamber (Fröhle and Roces, 2009).

The spherical shape of the chambers with fungus or empty and ellipsoid for those with garbage in the nest N1 of *A. sexdens* was similar to that described for the ant *A. sexdens*, in the forest, with a simple, closed structure and spherical or ellipsoid shape (Jacoby, 1950). On the other hand, garbage and fungus chambers with a semi-ellipsoid shape have been reported for this ant species with larger dimensions for the first ones (Pretto, 1996) and that of the chambers with fungus in *A. vollenweideri* nests were oval with bottom flat and those with garbage having a conical shape (Jonkman, 1980). It can be hypothetically inferred that the variation in the number and shape of chambers among species likely results from an interaction between the workers and the soil matrix in which they are building their nests. It is known that the fungus garden acts as a mold for chamber construction, and that its shape can be altered depending on the type of soil in which it is located (Camargo et al., 2013). Additionally, we can hypothesize that the decision to construct a new chamber in an incipient nest is primarily made by the workers, who expand the nest according to the colony's growth, promoting the relocation of the queen, the fungus garden, and the brood to the new chambers as needed. Regarding the soil matrix, it is known that bioturbation and nest construction by leaf-cutting ants produce two general types of landforms, which can be classified as excavational and constructional (Bétard, 2020). Excavational forms are directly associated with the construction of underground nests, and their complexity (size, shape, and depth) depends on the species and the age of the nest. Constructional forms, on the other hand, are characterized by mounds on the soil surface. The complexity of these structures also varies among species and may result from a combination of different landforms, such as the mounds of *Atta vollenweideri*. In addition to mounds and towers, the excavated soil is also mixed into the soil profile, lining the walls of chambers and galleries through the compression of soil aggregates against the walls (Cosarinsky and Roces, 2012), and also filling tunnels and chambers. All these behaviors can be classified as construction behaviors.

5. Conclusion

The format of the fungus chambers and the empty ones of *A. sexdens* was spherical and that of the garbage ellipsoids, the latter with branches similar to twigs and with larger dimensions than the formers. The inner sections of the tunnels of this ant nests were elliptical or circular with different dimensions. This is the first report of the nest architecture of the leaf-cutting ant *A. sexdens*.

Data Availability Statement

The research data analyzed in this study are not publicly available by any means.

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