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Nest Architecture and Animals Associated with *Neoponera verenae* (Forel) (Formicidae, Ponerinae)

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Abstract

The nests of ants *Neoponera* have chambers that can also be occupied by other species of organisms that can be tenants, visitors or prey. However, few studies have considered the assemblage of the associated species and described their composition. This study aimed to describe the architecture and catalog the visitors and prey species found in *Neoponera verenae* nests. Talcum powder was pumped inside eight nests to mark the chambers and tunnels. The nests were then excavated to describe the architecture and obtain measurements of chambers. The associated species encountered in the nests were collected and identified allowing us to obtain new records of visiting (*Linepithema* sp., cryptodesmid millipedes and *Neotropacarus* sp.) and prey taxa (membracids, apid bees and springtails) of *N. verenae*. Generally, nests had a single entrance hole and a depth of up to 42 cm. Nest chambers were found with three basic forms, elliptical, hangers and boot. Although studies show that this species can occupy abandoned nests of leaf-cutting ants, we found that the nests of *N. verenae* were more similar to those of *Ectatomma* ants. Indeed, we found one of the *N. verenae* nests was attached to a *Ectatomma edentatum* nest, leading us to suggest that *N. verenae* may occupy abandoned nests or displace other ants to occupy them.

Introduction

The building of nests by ants is a very costly activity in terms of energy and it has a key role in protecting the colony from predators and weather, as well as facilitating thermal regulation and helping the colony to fight pests and diseases (Pie et al., 2004; Tschinkel, 2015). In some cases, the nests may have chambers where there are larvae, pupae and eggs. They can be built into plant structures (roots, stem, leaves), on the soil surface, under the litter, or in deeper layers of soil reaching several meters in depth and can be formed of various construction materials available in the environment (Hölldobler & Wilson, 1990; Silva-Melo & Giannotti, 2010; Römer et al., 2020).

Nests can also serve as habitat for a variety of animals, both invertebrates (Pérez-Lachaud & Lachaud, 2014) and vertebrates (Harris & Savage, 2020). The fact that ants often present aggressive behaviors to defend their nests, makes nest interiors a safe location for other invertebrate species to take shelter (Laakso & Setälä, 1998; Hughes et al., 2008). It can be said that many of these tenants, in some way, depend on ants at least during part of their life cycle (Hölldobler

& Wilson, 1990). However, the relationships between the species that live inside these nests are not always harmonious. These habitats can present a complex network of interactions between tenants and those with hosts, which may include predations and parasitism (Parmentier et al., 2016). Currently, there are few studies showing which species of animals live with ants inside their nests (Pérez-Lachaud & Lachaud, 2014; Castaño-Meneses et al., 2019; Rocha et al., 2020; Mota Filho et al., 2021). Some of these studies are limited to certain groups of animals such as mites (Uppstrom & Klompen, 2011), Coleoptera (Päivinen et al., 2002) and Myriapoda (Stoev & Lapeva-Gjonova, 2005).

Ponerinae is a subfamily with a variety of nest architectures and nesting sites, being able to live from the subsoil (Silva-Melo & Giannotti, 2010; Guimarães et al., 2018) to the canopy of forests (Longino & Nadkarni, 1990; Camargo & Oliveira, 2012). *Neoponera* is a genus from this subfamily that often have nests located in hollow or decaying logs, healthy trees, epiphytes or underground (Araujo et al., 2019). In general, they are simple nests, with few chambers, little branched and preventing the organization of complex structures of food storage and maintenance of immature (Antonialli-Junior et al., 2015). Although some species may have nests with up to thousands of workers (Leal & Oliveira, 1995), most *Neoponera* species have nests that rarely surpass 200 individuals (Gobin et al., 2003; Yagound et al., 2017). For this reason, it is expected to find fewer (although equally important and poorly understood) visitor species in comparison with those found in larger nests of other genera such as the *Formica* (Härkönen & Sorvari, 2014). This difference is thought to be a result of the larger nests ants presenting a greater variety of microhabitats allowing more species to obtain shelter inside than small nest (Wilson, 1971).

Species of the *Neoponera* prey on small arthropods, although they may also act as scavengers (Wild, 2005). They also feed on seed elaiosomes and can have role as seed dispersers when transporting them to their nests (Horvitz, 1981). They have also been observed carrying liquid between the mandibles (Hölldobler, 1985) and visiting extrafloral nectaries (Byk & Del-Claro, 2010). Many species of this genus are specialized in termite predation (Mill, 1984; Leal & Oliveira, 1995), although there are also more generalist species in relation to the type of prey (Lachaud et al., 1984, Fresneau, 1985).

Neoponera verenae (Forel) is a species that can be found from southern Mexico to Paraguay occupying a variety of habitats, from rain forests to fields and pastures (Wild, 2005). However, almost all the information in the literature regarding this species appears under *Neoponera obscuricornis* (Emery) (Wild, 2005), which for some time has generated a few uncertainties about the characteristics of these species, particularly in Central and South America.

Previous studies have recorded this species occupying nests in tree trunks (Traniello & Hölldobler, 1984; Araujo et al., 2019), small rotting branches (Yagound et al., 2017), plant roots and clumps of grass in pastures (Wild, 2005). However, there has been no detailed analysis of the architecture of these nests. *N. verenae* is a species limited to making only slight modifications in natural cavities or dens built by other animals to build their nests, however, due to the space limitations that this strategy entails, *N. verenae* often performs migrations in search of new nest sites (Pezon et al., 2005).

This study aimed to describe some architectural characteristics of *N. verenae* nests, such as the number of chambers, their dimensions, shapes and spatial arrangement, depth, number and diameter of the entrance holes, in addition to cataloging the visitors and prey species found in them.

Materials and Methods

Eight *N. verenae* nests were collected from the campus of the São Paulo State University (UNESP), city of Rio Claro, São Paulo (22° 23' 40" S/ 47° 32' 44" W). The nests were found within an area covering about 30 ha, where excavations were allowed without interfering with other research areas on the campus. In addition, locations were selected where it was possible to visually locate the workers that were foraging. Some of these nests were already known from previous observations by the authors. Other were located by searching grassy and wooded places where biscuits and sausage were spread to attract workers of the species. They were followed to the entrance of the nest, which was then marked with colored ribbons until the day of excavation of the nest. Confirmation of the identification of the species took place after collecting the workers observed, prior to the excavation date. The identified workers are deposited in the Entomological Collection of the Department of Biodiversity (formerly the Department of Zoology) of the Biosciences Institute, in UNESP – Rio Claro Campus.

Nest excavation followed the methodology proposed by Antonialli-Junior and Giannotti (1997; 2001), as also used by Vieira et al. (2007) and Silva-Melo and Giannotti (2010). Only one nest (Nv1) was filled with epoxy cement following Tschinkel (2010).

Neutral talcum powder was pumped with the aid of a duster into the main entrance of the nests. Dusters are commonly used to pump poison powder into the nests of *Atta* and *Acromyrmex* species and the same dusters were also effective for pumping neutral talc into the nests of *N. verenae*. This strategy facilitated the visualization of tunnels and how they are connected to the chambers (Caldato et al., 2016).

To describe the nest architecture, we cleared around the main entrance to remove the soil cylinder where the nest was found. After isolating this cylinder, it was carefully excavated in vertical layers from the edges to the center of the cylinder with the use of a sharp trowel, until reaching the nest chambers. In this way, it was possible to prevent possible organisms present in the vicinity of the nest from mixing with those inside. If it was noticed that the nest continued to a depth greater than that initially excavated, the process was resumed to a greater depth. The excavation was completed when it was noted that there were no more deep chambers or tunnels. During the excavation process, we measured the height, width and length of the chambers as well as the diameter of the inlet and/or outlet (Antonialli-Junior & Giannotti, 1997; 2001; Caldato et al., 2016) and we made a sketch, in scale, considering the shape and arrangement of the chambers and tunnels of each nest.

In this study, we counted the *N. verenae* population in all nests except the Nv1 and Nv4 nests because in the first we used epoxy cement for the mold and ants were not collected from the second. The prey and visiting species were collected from the tunnels and chambers of the analyzed nests. Were defined as prey the individuals of other species that were found paralyzed or disjointed, as well as their parts, in the nest chambers. As visitors were considered the organisms of other species that were found inside the nest and seemed not to have suffered any type of predation or attack. The visitor and prey species encountered in the nests were collected and identified.

Results

The depth of *N. verenae* nests ranged between 6 cm and 42 cm ($\bar{X}$ = 25.125 cm, SD = 12.845 cm; n = 8). There was a single entrance/exit in all except for one nest (Nv2) that had three holes. The diameter of the entrance holes ranged from 0.7 to 3.0 cm ($\bar{X}$ = 1.437 cm, SD = 0.773 cm; n = 8) (Table 2).

The Nv1 nest is shaped like a boot and for presenting a single chamber, in a low depth and relatively small when compared to the chambers found in the other nests, it was deduced that it was in the initial stages of development. Before being excavated this nest was filled with epoxy cement, which provided a three-dimensional mold (Fig 1a).

The Nv2 nest was the only one with three entrances/exits. The first chamber had two branches, one leading to another two chambers and the second leads to a single chamber. Pupae were found just after the entrances to these lateral holes, they were also found in the chambers II, III and IV. Larvae were observed in the chambers I, II and IV. Prey remains were found in chamber IV (Table 2, Fig 1b).

The Nv3 nest had at its entrance a vertical tunnel leading to two chambers. Chamber I has an elliptical structure, whereas chamber II is boot shaped and was constructed next to a root (Fig 1c).

The Nv4 nest had an entrance/exit hole with a short tunnel that branches into two chambers lying on opposite sides, forming a hanger shape, with one side (chamber II) being closest to the surface (Fig 1d).

The Nv5 nest has a single entrance hole with a vertical tunnel leading to a chamber with a division and a branch leading to another two chambers. We did not record any tunnel connecting chamber II. Chamber III is a large ellipsoid and at the base has a connection tunnel that could be for a chamber to be built later (Fig 2a).

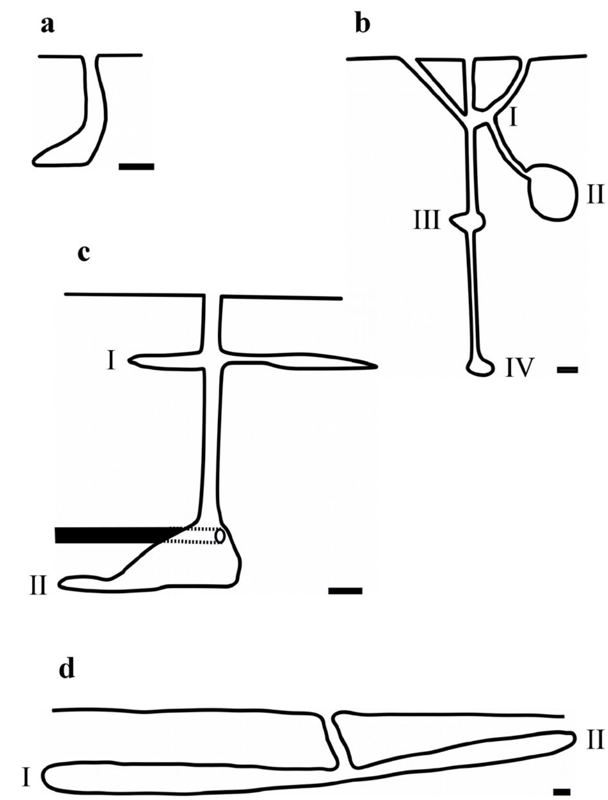

Fig 1. *Neoponera verenae* architecture nests. a: Nv1, b: Nv2, c: Nv3, d: Nv4. Scales 2 cm.

The nest Nv6 has the largest entrance diameter recorded and is connected to a short tunnel that leads to a boot shaped chamber (I), with larvae and pupae. Chamber II has a triangular

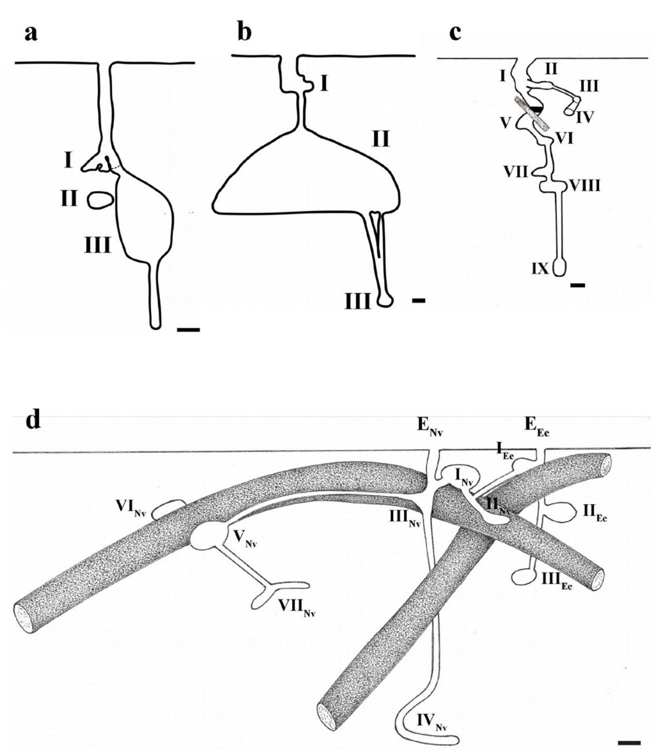

Fig 2. *Neoponera verenae*'s nest architecture. a: Nv5, b: Nv6, c: Nv7, d: Nv8. E_{Nv}: Entrance to the chambers where *Neoponera verenae* individuals were found. E_{Ec}: Entrance to the chambers where *Ectatomma edentatum* individuals were found. Scales 2 cm.

shape and at the base was earth mixed with dark colored organic matter. At the base of this chamber two tunnels extended vertically until they converge approximately 4 cm away from the chamber. Chamber III is reached after the junction of the tunnels and has the same shape as chamber II but is smaller. Chamber III was filled with pupae and larvae (Fig 2b).

The Nv7 nest has an entrance hole connected to a wide tunnel that leads to the chamber I and branches towards chambers II, III and IV. Chamber V was built next to a root and in the center is filled with earth, like a division. Chamber VI is a simple tunnel expansion, chamber VII has a slight lateral expansion and VIII is slightly rectangular receiving the upper tunnel from the side, which exits the chamber on the opposite side to the chamber IX. Waste was stored in chamber IX, which had a lot of decaying organic matter and associated animals (Table 2, Fig 2c).

The Nv8 nest, is similar to the hanger shape that was seen in Nv4, however it was built next to a root. This nest has a hole with a tunnel leading to a chamber (I_{Nv}), in the basal portion there were two tunnels, one goes toward the chamber III_{Nv}, the second branches into a smaller chamber (II_{Nv}) and an *Ectatomma edentatum* (Roger) nest (Fig 2d).

Chamber III_{Nv} of nest Nv8 is an expanded region in the vertical tunnel that branches horizontally giving access to the chambers V_{Nv}, VI_{Nv} and VII_{Nv}, the latter is branched, reaffirming the hanger structure. In this nest pupae were found at the end of the hook-shaped chamber IV_{Nv}. The larvae were found in chamber VII_{Nv}.

Inside the nests where *N. verenae* individuals were counted, we found eggs in three of them (Nv6, Nv7 and Nv8; $\overline{X}$ = 1,67 ± SD = 2,42; n = 6), larvae were present in all nests, except Nv3 ($\overline{X}$ = 11,5 ± SD = 8,31; n = 6), pupae, in turn, were absent only from Nv3 and Nv5 nests ($\overline{X}$ = 33,17 ± SD = 30,23; n = 6), while males were only found in Nv8 nest ($\overline{X}$ = 0,33 ± SD = 0,82; n = 6) and workers in all of them ($\overline{X}$ = 98,5 ± SD = 64,28; n = 6). No queens were found in any sample (Table 1).

Half of the eight nests had associated organisms or fragments thereof, totaling thirteen different taxa, of which seven (53.8%) were classified as prey. These organisms were mostly arthropods but were also found in one of the nests (Nv7) mollusks (Gastropoda) and nematodes. This was also the nest with the highest number of taxa found. Regarding arthropods, five distinct classes of this group were identified, mostly insects (orders Hemiptera, Hymenoptera, Lepidoptera and Coleoptera) found at different stages of development; but also, Diplopoda, Malacostraca (Isopoda), Entognatha (Collembola) and Arachnida (Acarina) (Table 2).

Table 1. Populations of *Neoponera verenae* in six nests.

Nest	Egg	Larva	Pupa	Male	Worker	Collection date
Nv2	-	25	76	-	54	21/03/2014
Nv3	-	-	-	-	98	01/03/2014
Nv5	-	10	-	-	75	03/04/2014
Nv6	1	13	31	-	226	03/04/2014
Nv7	6	7	36	-	61	10/04/2014
Nv8	3	14	56	2	77	10/04/2014

Discussion

Nest excavation followed by description and mapping enables the collection and counting of adult ants, their immatures and the other organisms present. This method is advantageous because it enables the collection of live specimens unlike the method used by Tschinkel (2010), in which all inhabitants of the nest are killed to obtain the mold.

In addition to the ants, other invertebrates were found in the nests of *N. verenae*. Our analysis did not identify the ecological role that each taxon plays within the nest or the importance of ants to their life cycle and survival. However, it was possible distinguish between possible preys and other associated animals. A variety of different animal species have been found associated with the nests of other *Neoponera* species, but some of the records made in this work are new to the group. As is the case with the presence of *Linepithema* sp. in two of the nests collected, milipedes of the family Cryptodesmidae, although there are records of presence of individuals of the same order (Polydesmida) in nests of other species of Ponerinae (Castaño-Meneses et al., 2019).

The presence of nematodes in nests is generally associated with parasitism between them and the ants (Poinar, 2012), even though its known that certain species of nematodes can also act as carriers of pathogens (Ishaq et al., 2021), or even commensals (Maschwitz et al., 2016) on certain ant species. However, records of nematodes in nests of *N. verenae* have not been found, even if rare records of their presence in nests of *Neoponera villosa* (Fabricius) are known (Wheeler, 1928). The confirmed association between *N. verenae* ants and mites of the *Neotropacarus* genus is also an unprecedented record. This genus is known for inhabit the surface of plants from different families (Ferla & Moraes, 2008; Zhang, 2012; Berton et al., 2019), which leads us to think that its presence inside a subterranean nest may be of something accidental, although it is impossible to affirm from our observations how these specimens reached this habitat. However, mites from other genera of the Astigmata group, to which *Neotropacarus* belongs, have already been found in nests of other Ponerinae ants (Castaño-Meneses et al., 2015), including species of *Neoponera* (Araujo et al., 2019).

The records of Isopoda coexisting as tenants in nests of other species of *Neoponera* (Triplehorn & Johnson, 2005) and also of other Ponerinae ants (Almeida & Queiroz, 2015; Castaño-Meneses et al., 2019) are recurrent. The same can be said about the association with mites of the Laelapidae family (Castaño-Meneses et al., 2015; Rocha et al., 2020), including the record of this group within nests of *N. verenae* (Lopes et al., 2014).

Table 2. Characteristics of *N. verenae* nests and associated animals found inside them. H = height, W = width, L = length.

Nest		Chambers dimensions (cm)									Total depth of the nests (cm)	Entrance hole diameter (cm)	Number of entrance holes	Organisms presents in the nest
		I	II	III	IV	V	VI	VII	VIII	IX				
	H	4												
Nv1	W	1 to 3	-	-	-	-	-	-	-	-	6	0.7	1	-
	L	2												
	H	2	6	2	2									
Nv2	W	3	5	3.5	3	-	-	-	-	-	35	1	3	**Prey** Insecta: Hemiptera (Membracidae nymph)
	L	2	5	14	3									
	H	0.5	3.5											
Nv3	W	14	10	-	-	-	-	-	-	-	16	1	1	-
	L	6	4											
	H	1.5 to 3.5	1.5 to 2.5											
Nv4	W	40	30	-	-	-	-	-	-	-	11	1.3	1	-
	L	3.5	2.5											
	H	1.5	1.5	8										
Nv5	W	3.5	2.5	5	-	-	-	-	-	-	25	1	1	**Visitor** Insecta: Hymenoptera: Formicidae (*Linepithema* sp.) Diplopoda: Polydesmida (Cryptodesmidae)
	L	3	1.5	12										
	H	2 to 3	14	2.2										
Nv6	W	2.75	32	2.4	-	-	-	-	-	-	42	3	1	-
	L	3	14	1.5										
	H	1	1	0.8	0.8	6.5	1.5	1.7	1.7	2.5				
Nv7	W	3	4	1	1.25	2.5	1.5	1.5	4	2	33	2.2	1	**Visitor** Nematoda Insecta: Hymenoptera: Formicidae (*Linepithema* sp.) Malacostraca: Isopoda Arachnida: Mesostigmata (Laelapidae); Sarcoptiformes: Acaridae (*Neotropacarus* sp.) **Prey** Mollusca: Gastropoda Insecta: Lepidoptera (larvae), Coleoptera (fragment), Hymenoptera: undeterminated (fragment); Apidae (fragment) Entognatha: Collembola
	L	?	3	?	?	8	4	5	6	5				
	H	3	1	2	1	2	2	3						
Nv8	W	3.5	3	2.75	6	3	3	6	-	-	33	1.3	1	**Visitor** Diplopoda: Polydesmida (Cryptodesmidae)
	L	7.5	?	7	?	2	6	7						

Our findings showed a clear lack of specialization in the diet of *N. verenae*. Some of the prey species found inside the nest are similar to those from other *Neoponera* species. Lepidoptera larvae have been recorded as prey for *N. verenae* previously by Longino (2010), also serving as food for other *Neoponera* species, as *Neoponera apicalis* (Latreille) (Fresneau, 1985). *N. obscuricornis* were observed preying on Hemiptera nymphs (Sujii et al., 2004), however predation on Membracidae is something new, being known only in other groups of poneromorph ants (Arias-Penna, 2008), the same can be said in relation to the capture of apid bees (Arias-Penna, 2008; Ostwald et al., 2018) and other hymenopterans as ants (Arias-Penna, 2008; Tofolo et al., 2011).

Published studies on *Neoponera* nests located in cocoa plantations and on bromeliads have already pointed out the occurrence of springtails living in the nests (Triplehorn & Johnson, 2005; Castaño-Meneses et al., 2015; Araujo et al., 2019). In addition, there are several records of other species of Ponerinae preying on springtails (Brandão et al., 2015), but this had not yet been registered for *N. verenae*.

Predation on beetles is known for *N. apicalis* (Fresneau, 1985) and foraging ants of the species *N. obscuricornis* were observed attacking beetles in the Brazilian Cerrado (Byk & Del-Claro, 2010).

The architecture of *N. verenae* nests is very diverse, but we observed similarities between them. The nests are most often constructed with a single entrance orifice - as well as those found by Araujo et al. (2019) in cocoa agroforestry plantations – up to 3 cm in diameter, with vertical chambers up to a depth of 42 cm. However, Delabie et al. (2008) reported that *N. verenae* ants can construct nests that may reach up to 150 cm in depth.

Nv8 has a tunnel between chambers III_{Nv} and V_{Nv} that follows the path opened by a root, which may be the result of an opportunistic strategy adopted by the ants to take advantage of existing cracks and openings, thereby saving energy. This fact may explain why the Nv8 nest does not present the architectural structures observed in the other nests. This nest was also connected to an *Ectatomma edentatum* (Roger) nest on a branch of a blind ending side chamber, which had ten workers, nine pupae and one larva.

According to Delabie et al. (2008), *N. verenae* can occupy the abandoned nests of leaf-cutter ants or termites. But when we compare the architectural structures of *N. verenae* nests with those of some fungi cultivating ants we saw that the nests of *N. verenae* are not similar to *Mycocepurus goeldii* (Forel) and *Mycocepurus smithii* (Forel) (Rabeling et al., 2007), *Mycetagroicus inflatus* (Brandão & Mayhé-Nunes) (Jesovnik et al., 2013), *Acromyrmex ambiguus* (Emery) (Bollazzi & Roces, 2007), and *Acromyrmex rugosus* (Smith) (Verza et al., 2007), and totally different from *Atta bisphaerica* (Forel) (Moreira et al., 2004).

It is possible that *N. verenae* use nests built by other species of insects or ants. We believe that the nests of *N. verenae* are more similar to those of *Ectatomma planidens* (Borgmeier) (Antonialli-Jr & Giannotti, 2001), *Ectatomma brunneum* (Smith) (Lapola et al., 2003) and *Ectatomma vizottoi* (Almeida Filho) (Vieira et al., 2007). This similarity comes from the arrangement of the chambers along the light from the entrance/exit hole, but according to these authors these nests are very deep and have chambers with appendices.

As the places where the nests were collected had little or no litter, none of the nests had an epigeic construction pattern, covered by litter, or using decomposing plant material (*e.g.* trunks, palm leaves or dry fruits) as nest substrate seen in other surveys on *N. verenae* (Delabie et al., 2008; Araujo et al., 2019). A further evidence of the plasticity of architecture found for nests of this species and the non-dependence of this type of microhabitat for nesting.

The absence of a clearer construction pattern and the fact that one of the nests is attached to an *E. edentatum* nest leads us to suggest that *N. verenae* may occupy abandoned nests or even displace other ants to occupy part or all of them. To test this hypothesis, it is interesting to carry out studies that can follow the development of nests of *N. verenae* and verify the occurrence of more nests of this species attached to nests of other ants, or even of other organisms.

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Authors' Contribution

Conceptualization: ASM, EG, HRM
Methodology: HRM, ASM, EG
Validation: ASM, HRM, EG
Formal Analysis: ASM
Investigation: HRM, ASM, EG
Resources: EG, ASM, HRM
Data curation: HRM, ASM
Writing-Original Draft: HRM, ASM, EG
Writing-Review & Editing: HRM, ASM, EG
Visualization: HRM, ASM, EG
Supervision: EG, ASM
Project administration: EG, ASM
Funding acquisition: ASM, EG

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