



A preliminary study of nest structure and composition of the weaver ant *Polyrhachis (Cyrtomyrma) delecta* (Hymenoptera: Formicidae)

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ABSTRACT

Polyrhachis weaver ants build their nests from vegetation bound together using silk produced by their larvae. Here we provide a pilot study of the composition and the physical structure of three arboreal silk nests of *Polyrhachis (Cyrtomyrma) delecta* based on examination of three colonies. We found broadly similar nest architecture and size of the nests with each containing six or seven identifiable chambers, and describe the distribution of ants of different castes and life stages between them. We also note the construction of silk 'girder' structures, which spanned larger chambers, and we hypothesize that these provide additional strength to the internal nest structure. This study highlights the importance of more detailed investigation of the internal nest structure and composition in *Polyrhachis*, and other weaver ant species, which will help to develop our understanding of this specialized form of nest construction and nesting habits in a diverse group of ants.

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Introduction

The ability of social insects to locate suitable nesting sites and, through manipulation of the environment, to construct often highly complex nests is key to the success of the colony and of social insects in general (Hölldobler and Wilson 1990). In ants, nests can range in size and complexity from the vast underground networks of *Atta* leaf-cutting ants, to a whole colony of *Temnothorax* contained within a single acorn (Hölldobler and Wilson 1990). The nesting habits of organisms are an important factor in their life history and a powerful driver of their morphology and ecology (Jeanne 1975; Mikheyev and Tschinkel 2004). The architecture of the nests themselves is believed to be key in the evolution of division of labour, which has contributed to the ecological success of ant societies (Hölldobler and Wilson 1990). The internal structure of a nest and the internal arrangement of ants and the brood within it can potentially also have important implications for the spread of infectious diseases within colonies (Schmid-Hempel 1998; Naug and Camazine 2002). Social insects may be particularly vulnerable to parasites because of the very high population densities, homeostatic environmental

conditions and low genetic diversity within colonies, which contribute to an increased risk of parasite transmission. In leaf-cutting ants, waste management tasks are partitioned spatially and between castes, which helps to isolate the main colony from the increased risk of contamination (Bot et al. 2001; Waddington and Hughes 2010). Similarly, compartmentalization between chambers within the nest may help to prevent transmission of parasites to vulnerable aspects of the colony such as the queen or brood (Pie et al. 2004; Boomsma et al. 2005).

Polyrhachis Fr. Smith is a diverse genus of ants within the subfamily Formicinae with over 600 species widely distributed across Africa, Asia and Australasia. Commonly termed 'weaver ants', many species form arboreal nests constructed from vegetation bound together with silk produced by their larvae, but may vary widely from species with subterranean nests formed from intertidal mangrove mud to lignicolous and lithocolous species (Robson and Kohout 2007). There is also an extreme range of colony sizes and compositions from very small colonies with just a few tens of individuals, through to colonies with almost a million workers (Liefke et al. 1998; Dornhaus et al. 2012). Colonies tend to be polydomous, and in some species may also be polygynous with multiple de-alate queens within a nest (Liefke et al. 1998; van Zweden et al. 2007). Like other formicines, weaver ants produce acidic venom from their venom gland, which they can use to disinfect themselves and their brood (Graystock and Hughes 2011; Tragust et al. 2013; Tranter et al. 2014). Additionally, *Polyrhachis* and *Oecophylla* weaver ants use this venom to maintain acidic conditions of their nest silk (Tranter et al. 2014; Tranter and Hughes 2015). The general nesting habits of these ants have been well documented (Kohout 2000, 2012; Robson et al. 2015) and were recently set into a phylogenetic framework, broadly describing patterns of weaving behaviour and basic nest composition (Robson and Kohout 2005, 2007). There has been a comprehensive study of the unusual nesting habits of the estuarine species *Polyrhachis* (*Chariomyrma*) *sokolova*, as well as brief details of mainly external nest architecture, and records of colony composition for a few other *Polyrhachis* species (Nielsen 1997; Jinfu and Jue 1996; Liefke et al. 1998; Downes 2015). However, detailed observation of the finer scale structure and colony composition of *Polyrhachis* nests is less well documented, especially considering the large number of species in the genus and the diversity of nesting habits. Here we provide some preliminary information on this from three nests of the arboreal and silk weaving species of the Australian weaver ant *Polyrhachis* (*Cyrtomyrma*) *delecta*.

Material and methods




Ants were identified using keys available in Kohout (2006). Three nests of *P. delecta* were collected from around Centenary Lakes (16.902°S, 145.749°E), Cairns, QLD, Australia in July 2014. The nests were externally formed from interwoven leaves hanging in vegetation approximately 1.5 m above ground and were suspended at a single point. At each site the nests collected were the only nests visible in the vicinity. Nests 2 and 3 were approximately 20 m apart, and Nest 1 was located about 40 m from either of the other nests; none of the nests was therefore found on the same plant as the others. Nests were measured externally about three axes to give a height, breadth, width measurement using a 30-cm ruler. Nests were all approximately ellipsoid in shape and estimated

volumes were calculated using the formula $V = 4/3\pi abc$, where $a = \frac{1}{2}$ height, $b = \frac{1}{2}$ breadth, $c = \frac{1}{2}$ width. The whole nest was collected by cutting the branch above the nest and gently releasing the nest into a plastic container. Returning worker ants were collected individually for a period of 15 min after collection of the nest and stored separately in 95% ethanol. This collection method resulted in minimal disturbance of the ants. The nest was then left for 6 h during which time the few ants that had emerged during collection returned to within the nest. The whole nest was then rapidly chilled by placing it in the freezer at -20°C , and kept there for 3 h. The nest was then removed from the freezer, measured externally, and carefully dissected. The position and size of chambers within the nest were recorded, and their contents – queens, gynes (alate queens), males, workers and brood – were collected in ethanol for later counting under a stereomicroscope. Although every effort was made to minimize disturbance of the nest before dissection it was not possible to determine the extent to which ants within the nest may have repositioned during procedures. Therefore any positional data of castes within the nest should be treated cautiously. *Polyrhachis delecta* larvae do not spin larval cocoons, the loss of which is thought to be restricted to the *Cyrtomyrma* and *Myrmatopa* subgenera, and pupae are exposed within the nest (Robson and Kohout 2007; Robson et al. 2015). Downes (2015) reported that it is possible to discriminate between incipient workers and incipient sexuals in the closely related *Polyrhachis australis* using the presence of wing buds on exposed pupae, but we were not able to reliably do so here for *P. delecta*. After removal with soft forceps of all ants and brood, the internal nest structure was recorded with sketches and photographs (Canon 7D and Canon MPE-65 mm or 100 mm f/2.8 macro) as the dissection progressed. Samples are stored at the University of Sussex, UK.

Results

Nests 1 and 2 were similar in their external structure, dimensions and construction, whereas Nest 3 was larger and more spherical in shape (Table 1). All three nests were formed from five or fewer leaves at the terminus of a hanging branch, with the leaves slightly folded and woven together with silk and carton material, and in some cases (c. 20%) split along veins (Figure 2C). All nests had one entrance located at the bottom of the nest. Internally, nests were composed of one or two large chambers, usually formed as one whole section between two leaves, and a number of smaller chambers towards the periphery (Figure 1). These chambers were lined with silk sheets, which varied in thickness from so thin as to be almost transparent to the approximate thickness of standard 75 gsm copy paper (100 μm). Three of the larger chambers possessed cylindrical protuberances, which we term here ‘girders’. These girders emerged from the inner wall and spanned the chamber, and were formed from tightly layered silk (Figure 2A,B). A single large girder was present in Chamber 4 of Nests 1 and 2 and a smaller girder was also observed spanning the walls of Chamber 2 in Nest 2. Nests 1 and 2 contained similar numbers of workers, alate queens and brood (Table 2; Figure 2D,E). Nest 3 however had fewer workers and brood, no de-alate queens and very few alate queens present, unlike the other two nests. There were some similarities between the three nests in the locations in which most of each of the castes were found (Figures 1 and 3). This was most evident between Nests 1 and 2, which shared a

Table 1. Information on external and internal colony structure of three nests of *Polyrachis delecta*.

Nest	External dimensions	Internal chamber details		
	(height × width × depth)	Count (<i>n</i>)	Chamber	Volume (%)
1. 	Formed of three leaves 140 × 70 × 65 mm volume: 333.53 cm ³	6	1	10
			2	20
			3	10
			4	44
			5	10
			6	5
2. 	Formed of five leaves 135 × 75 × 60 mm volume: 318.09 cm ³	7	1	10
			2	20
			3	5
			4	35
			5	10
			6	10
			7	10
3. 	Formed of three leaves 110 × 85 × 80 mm volume: 391.65 cm ³	6	1	10
			2	20
			3	25
			4	25
			5	10
			6	10

Numbering detailed in Figure 1. Approximate volumes are calculated from dimensions.

more similar physical structure. The de-alate queen in Nests 1 and 2 was located in the largest chamber of the nest, which also contained a large number of eggs and small larvae. The males tended to be located in chambers towards the nest's middle. Workers were found in all chambers throughout the nest but there was some indication that they may be more concentrated in chambers adjacent to nest entrances, and those chambers towards the top of the nest (Table 2). These uppermost chambers also contained large numbers of alate queens and larger larvae.

Discussion

We present here the first observations and descriptive data on the structure and composition of three nests of the weaver ant *P. delecta*. There was evidence of segregation of castes within the various chambers in the nest and similarities in their spatial position between nests. We also noted the inclusion of tightly wrapped sections of silk, that we term here 'girders', which horizontally spanned a number of the larger chambers. These girders were extremely rigid compared with the rest of the nest construction and we hypothesize that they function to provide internal support to stop the lateral compression and collapse of inner chambers and the nest as a whole.

Many ant colonies undergo seasonal variation in their size and composition, which is often best seen in the different rates of caste production (i.e. workers versus sexuals) or the season in which brood may tend to be produced. Downes (2015) demonstrated seasonal fluctuations in the colony composition of *P. australis*. In that study, alate queens and alate queen pupae were mostly present only from July to December. In our study, conducted in July, we also found the presence of alate queens in quite high numbers. In addition, we found generally similar nest sizes to Downes (2015), with the exception of males, which were more numerous in the colonies in our study. Compared with other

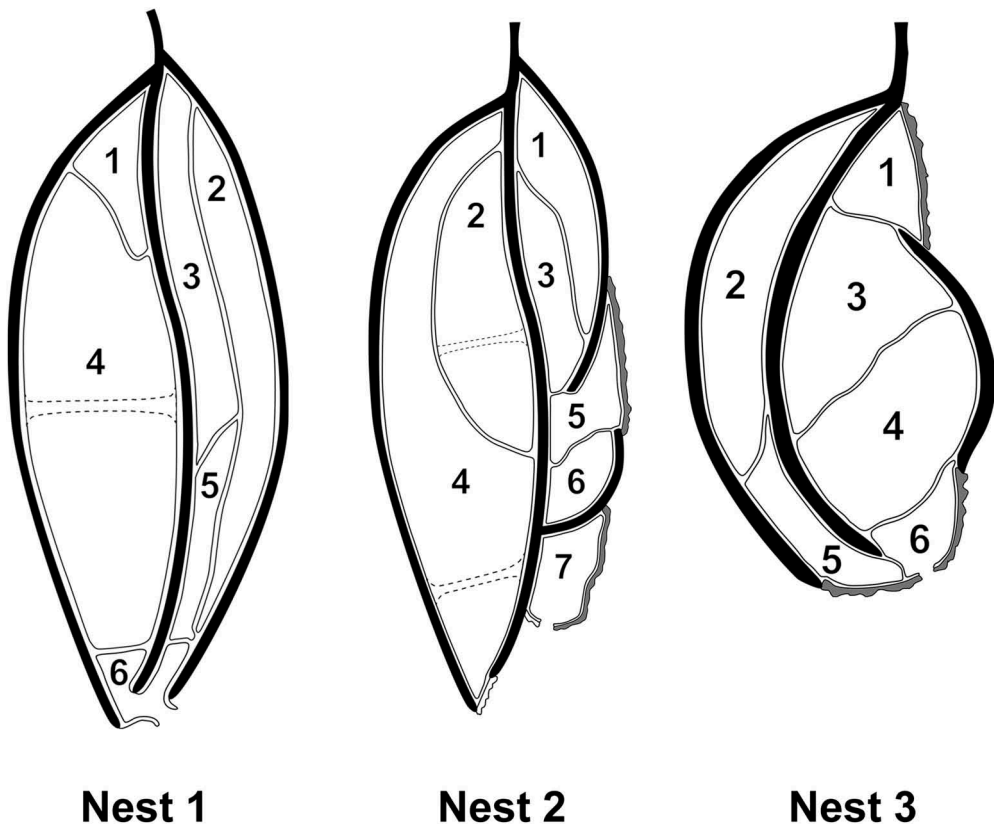


Figure 1. Lateral view schematic illustrations of the internal chamber arrangement of three nests of *Polyrhachis delecta* weaver ants. Chambers are labelled 1–7. Nests were suspended from vegetation at the top and thick black lines show the core arrangement of leaves, which were divided into chambers through construction with larval silk (thin lines). Sections with wavy outlines in grey on the outer surface of the nest indicate areas constructed from carton. Internal structures with dashed lines indicate the position of internal ‘girders’. Nest openings are portrayed oriented towards the lower right of each nest.

Polyrhachis species these nest populations are small overall for the genus, many species of which have thousands of workers, but are more representative of species within the *Cyrtomyrma* subgenus as a whole (Dorow et al. 1990; Dorow 1995; Glaser 1997; Liefke et al. 1998). In this study we estimated that the proportion of foragers constituted around 5–18% of the total worker force, although returning foragers were only collected for 15 min after nest collection. In *Odontomachus brunneus* the foraging population found outside the nest was estimated to be 77% of the total workforce (Hart & Tschinkel 2012), much higher than we estimated here, but in general it is unknown quite how the proportions of foragers varies depending on ant species or overall colony size (Tschinkel 1999).

As the size of nests and number of chambers increases, the chance of a complete mixing of colony members decreases and so larger nests may promote colony complexity through task differentiation or protection against disease through compartmentalization (Sendova-Franks and Franks 1995; Naug and Camazine 2002; Naug 2008; Konrad

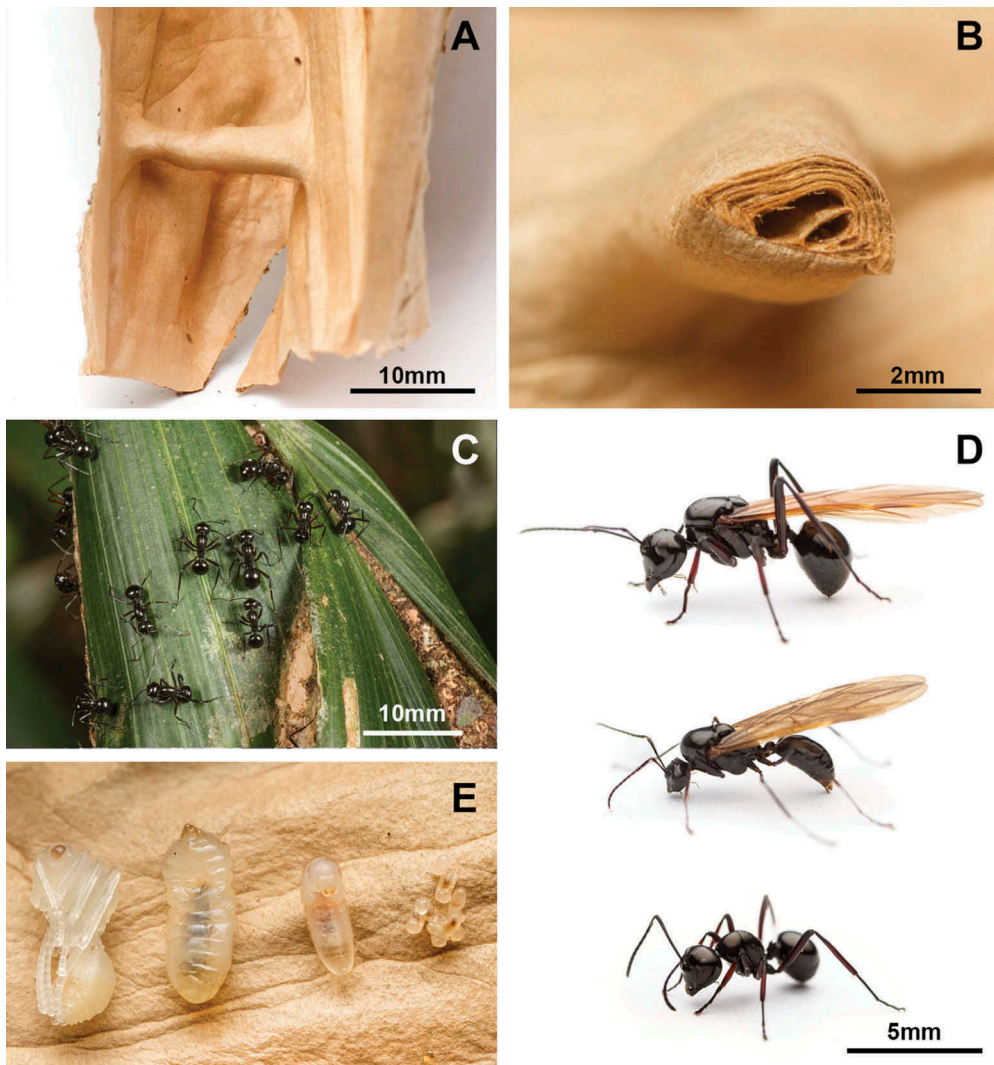


Figure 2. Photographs detailing a silk support structure ('girder') spanning a chamber within a nest (A), a cross-section of the 'girder' (B), a view of the outside of Nest 1 showing workers on sections of the folded leaf with an area of visible carton in the bottom right (C), examples of an alate queen (top), male (middle) and worker (bottom) of *Polyrhachis delecta* weaver ants (D), and examples of the various brood stages including a pupa (left) and variously sized larvae (middle to right) (E).

et al. 2012). In this study there were indications of some degree of compartmentalization of nest components to different chambers within the nest, although the potential for relocation of ants between collection and dissection, and the fact that the study was limited to only three nests means that these data must be treated cautiously. As with other social insect nests (Kugler and del Hincapie 1983; Longino 1991; Ito et al. 1994; Baracchi and Cini 2014), the brood, and especially the queen, tended to be located away from the periphery of the nest, and usually away from the nest entrance. Additionally, nest architecture is important in producing correct internal nest microclimates and

Table 2. Overall details of the composition of ants in three nests of *Polyrachis delecta*.

Caste or life stage	Nest 1							Nest 2							Nest 3						
	By chamber (%)							By chamber (%)							By chamber (%)						
	1	2	3	4	5	6	Totals	1	2	3	4	5	6	7	Totals	1	2	3	4	5	6
Adult ants																					
De-alate queens	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alate queens	79	14	27	42	11	3	4	92	17	22	27	21	3	9	1	6	33	67	0	0	0
Males	38	63	16	21	0	0	0	37	22	41	32	3	0	3	0	15	40	0	60	0	0
Workers																					
Within colony	394	12	13	7	33	12	23	446	16	12	12	19	24	11	7	183	4	11	10	28	39
Outside colony	27							19							33						
Total	421						465								216						
Brood																					
Pupae	37	35	14	30	22	0	0	64	33	14	28	22	3	0	0	18	12	88	0	0	0
Large larvae	53	0	17	17	66	0	0	21	14	5	14	67	0	0	0	10	30	70	0	0	0
Small larvae	19	0	0	0	100	0	0	35	0	23	0	77	0	0	0	5	0	100	0	0	0
Eggs	yes						yes														
							no														

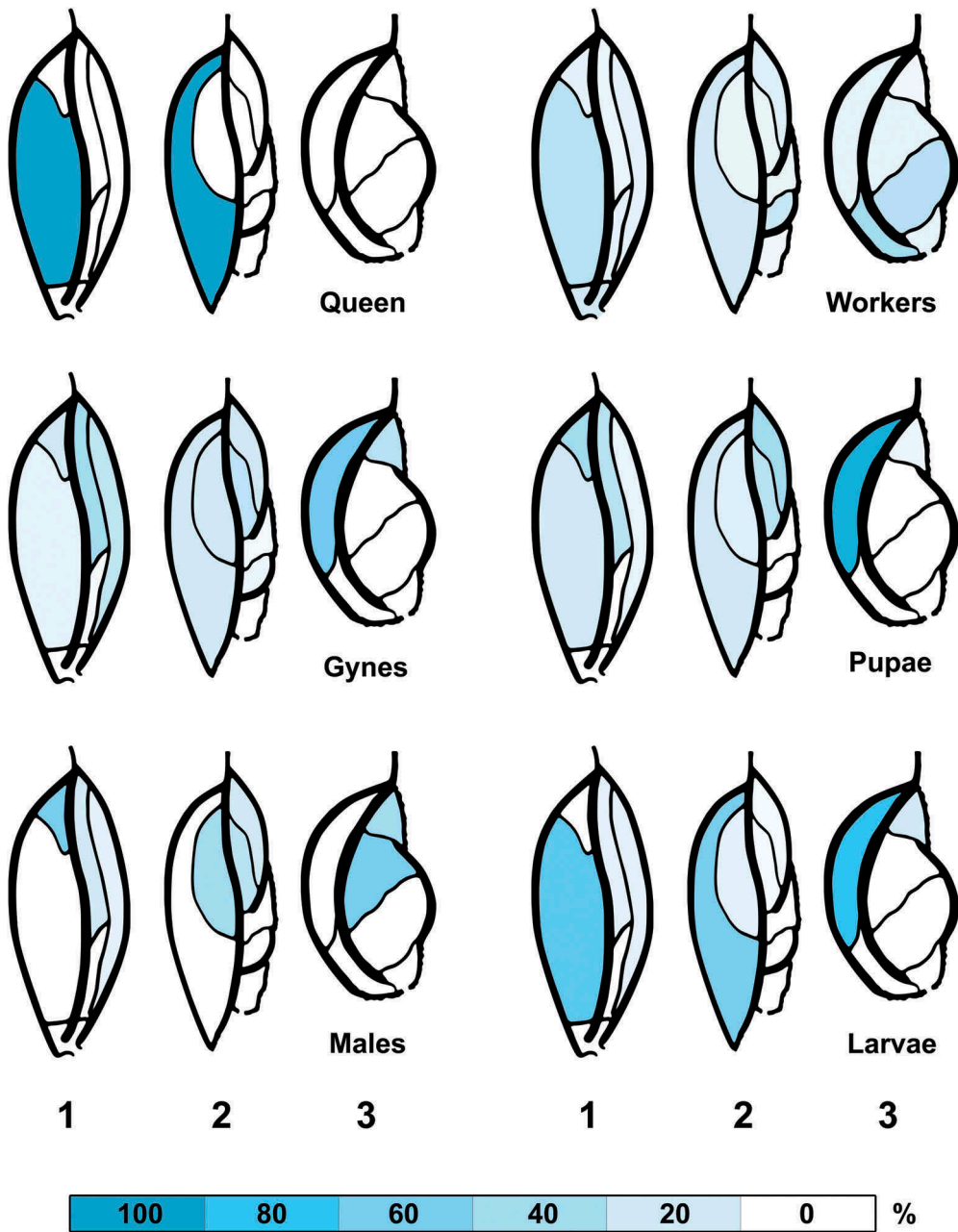


Figure 3. Panel showing the percentage of each ant life stage within each chamber of each of three nests of *Polyrhachis delecta* weaver ants.

brood may be moved within colonies so as to raise them at the correct temperature, which may be in part responsible for the location of brood observed in this study (Sendova-Franks and Franks 1995; Tschinkel 1999). Further investigation of more *P. delecta* nests is needed to confirm the descriptive data provided here.

Polydomy occurs in a number of *Polyrhachis* species, some of which have been described as supercolonial (Yamauchi et al. 1987; van Zweden et al. 2007), and it is possible that the presence of the queenless, brood-bearing and otherwise healthy nest in this study is evidence for this in this species. Hence it is hard to know if the assemblages collected here represent distinct colonies or, as we term them here, just one of possibly many ‘nests’ that comprise the colony as a whole. As three nests were collected for this study and all were relatively small, collected from only where nests were readily discoverable and easily collected, and from a limited geographic locality, it is likely that there is selection bias in these results. Larger colonies or those located higher in the vegetation, or at a different location, may differ significantly in their structure and composition. It is likely that there will have been some internal relocation of ants within nests between collection and dissection, so the data on the intranidal location of ants needs to be treated cautiously. Nonetheless Nests 1 and 2, which were similar in size and structure, seemed to also share similarities in their spatial location of ants.

Although general nesting patterns are quite well studied across *Polyrhachis* species, this study provides the first descriptive data of the interesting structure of *P. delecta* nests. We hope that this work will stimulate future more detailed studies on nest structure and composition to further explore the intricacies of this specialized form of nest construction, which may help to elucidate evolutionary patterns of nest-building and habitat preference in this highly diverse genus of ants.

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