

Species composition and nesting habits of ants in a hill-country home garden in Sri Lanka

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ABSTRACT. This study attempts to identify the ants nesting in a home garden in the hill-country of Sri Lanka and to describe their nest morphology with a view to using the same for their identification. A total of 21 ant species were recorded from the home garden by a combination of methods, and of these, eight also occurred indoors. A total of 1,363 nests belonging to 18 species inhabiting the home garden were encountered, and their external morphology is described. Nest longevity of these species varies greatly, from over 25 years in *Myrmicaria brunnea* to only a few weeks in some species. Only five species of ants nested indoors; selecting damp, shady and hidden locations and moving readily upon disturbance.

Keywords: Formicidae, species composition, nesting types, home garden

INTRODUCTION

Ants are the most conspicuous group of invertebrates in home gardens as well as most other commensal environments in Sri Lanka. The large number of individuals in many ant colonies, and their persistence almost throughout the year, make ants amenable to home-based study. The numerous roles ants play in urban areas, as invasive cosmopolitan species, as pests (Lee 2002; Dias 2006a; Warner *et al.* 2009) under certain conditions and as representatives of biological diversity, make it important to understand them.

The first comprehensive study on the ants of Sri Lanka, formerly Ceylon, was by Bingham (1903) who recorded 498 species in 79 genera belonging to five subfamilies. Since then, very little work has been done on the systematics of Sri Lankan ants. The 65,610 km² island of Sri Lanka has a rich fauna and flora, with several endemic taxa, including the ant genera *Aneuretus* Emery in the monotypic subfamily Aneuretinae (Wilson *et al.* 1956) and *Stereomyrmex* Emery in the Myrmicinae.

In recent times, there have been several reports on the diversity and distribution of ants in selected areas of the country by Dias (2002, 2003, 2006a, 2006b), Dias and Chaminda (2000) and Dias and Perera (2005, 2007). Amarasinghe and Edrisinghe (2006, 2007) recorded 22 ant species in a multipurpose agricultural farm in the central hills of Sri Lanka. Intensive field sampling within and along the boundaries of the Sinharaja Man and Biosphere (MAB) Reserve in southern Sri Lanka have recorded several more species and subfamilies of ants, of which some are new to science (Gunawardene 2007; Gunawardene *et al.* 2008).

Information on ants of home gardens and households is lacking. Also, the nest morphology of most tropical ants, including those in Sri Lanka, has not been intensively studied and hence, very little information is available (Wilson *et al.* 1956; Jayasuriya & Traniello 1985). Certain features of nest morphology may shed light on species identification of ants, a challenge which is very complex in this ubiquitous group.

The aim of this home-based study was to provide baseline information on ants that are

likely to be encountered in day-to-day life in the study region. The specific objectives were to inventory the ant species inhabiting a home garden and household in the hill-country wet zone of Sri Lanka, and to record the nesting sites and external nest morphology over a period of time.

MATERIALS AND METHODS

Study area

The study was carried out in a home garden in Nawalapitiya, located at 7°31' N and 81°32' E, in Kandy District in the hills of Central Province, Sri Lanka. Nawalapitiya is at an elevation of 612 m and receives a mean annual rainfall of 4,000–5,000 mm (Maplandia.com 2009). The average temperature ranges from 24 to 26 °C (Cherith International 2009).

The home garden studied was approximately 4,048 m² in area and was in a semi-urban neighbourhood on a small hill. It was bounded by a railway to the west and a major road to the north. Abandoned cultivated areas on the east and south sides were adjoined by a footpath at the edge of the homestead. The home garden can be considered typical for the neighbourhood. It was landscaped about 25 years ago and has three levels

(Fig. 1): an upper residential house and front garden (Habitat 1) (1,011 m² in extent), a central unattended grassland (Habitat 2) (1,214 m²) and a lower sloping garden to the north of the house (Habitat 3) (1,336 m²). Several footpaths form the boundary and traverse the home garden (Habitat 4) (215 m²).

The front garden (Habitat 1) had been levelled by dumping soil to form a tightly packed hard surface. The borders of the front garden were planted with roses, dahlias and other common flowering plants. Apart from these plants, the major part of the front garden was bare. Habitat 2 was formerly a cultivated site, later abandoned, and had become a grassland. The grass comprised mostly guinea grass, *Panicum maximum*, and was subjected to intense burning three to four times a year. Habitat 3 was a relatively undisturbed area with a dense ground cover of ferns: largely *Nephrolepis* and *Dennstaedtia* spp. Leaf litter accumulates in this area throughout the year. Several mature, common home-garden trees such as *Artocarpus heterophyllus* (jackfruit), *Artocarpus altillus* (breadfruit) and *Persea americana* (avocado), which had an average height of about 12–16 metres, were present and the canopy cover in this area is about 80%. The house was about 25 years old, had a cement floor and wooden furniture.

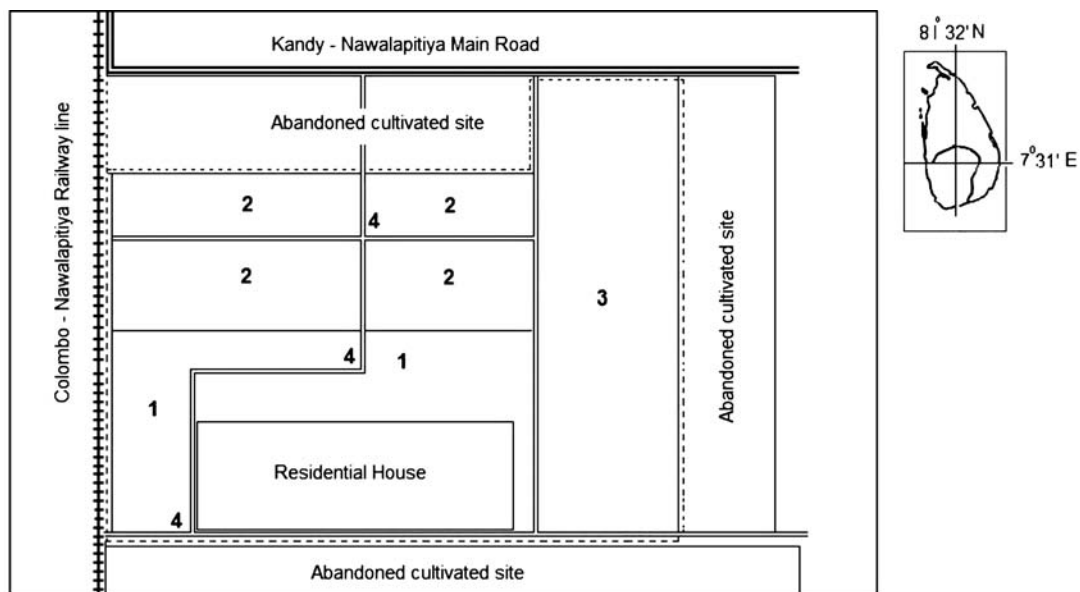


Fig. 1. Map of home garden showing study habitats. Location of study site in Sri Lanka.

Study methods

The study was conducted from November 2007 to January 2009. Ants were collected monthly over a 15-month period; all locations were examined at different times of the same day to reduce the influence of weather or time. Several methods were used for collection and sampling of ants. Hand collection was conducted in all areas of the home garden and the house, from nests, trails, ground and low vegetation. In each habitat of the garden and the house, paper squares baited with fish, sweet biscuit and sesame seed were set alternately along a 4 m transect at 0.5 m intervals, with three of each bait type, during daytime. Ants attracted were collected 30 minutes after the placement of baits. Ten pitfall traps were laid within three 2 x 5 m² plots in each habitat, on either side of another 4 m transect, at 1 m intervals. A standard plastic cup of 6 cm mouth diameter, filled with 70% ethanol, was used as a pitfall trap. An inverted lid with large triangular cuts along the lid margin was used to keep out rain. After 3 days, ants were sorted from the material collected in the cup. Leaf litter from each garden habitat was extracted using a mini-Winkler sack once each month; two samples were collected from two different locations in each habitat, 5 m apart from each other, and each sample, from an area of 1 x 1 m, was removed, sieved and hung in a sack for one week.

The home garden and the house interior were closely examined for ant nests regularly. Nests encountered were carefully examined and the following details were recorded: (i) entrance diameter, (ii) number of entrance holes, (iii) area of the “crater” (the ring of excavated soil around the nest entrance), (iv) approximate size of soil pellets around the entrance, and (v) shape of the tumulus and type of soil excavated. Soil type at the ant nest was identified according to the IFAS Soil Textural Triangle (Brown 2003). A sample of ants comprising several individuals representing the different castes (major and minor workers, queen and winged males) were collected from each nest into plastic vials containing 70% ethanol and stored for identification. Abandoned nests were excavated by making a vertical cut adjacent to the entrance hole.

Nest density in each habitat of the home garden was determined by counting the number of nests in a defined area (2 x 5 m² plot). The 2 x 5 m² plots were selected from the centre of Habitats 1, 2 and 3 and in Habitat 4, within the footpath. In addition to the nest density, the species inhabiting the nests were recorded.

All nests encountered were grouped into seven major categories based on the nesting habits: subterranean nest without above-ground structure, subterranean nest with above-ground structure (a prominent cone or mound surrounding the nest entrance), above-ground concealed nest (constructed entirely on the ground, beneath stones or wood), arboreal nest (made with silk among living tree leaves), lignicolous nest (constructed in or outside the stems of living plants and among decaying leaf litter), lithocolous nest (constructed within rock or cement crevices), and indoor nest (Robson & Kohout 2007).

Selected ant specimens were point-mounted and curated according to standard procedure for identification. Identification was made to generic level using keys of Bolton (1994), and to species level using reference ant collections deposited in the Department of Zoology, University of Peradeniya by Ms. N. Gunawardene who worked on the ants of lowland wet forest of Southwest Sri Lanka for her PhD study. Descriptions given in Dias (2002) and the reference ant collection at the National Museums Colombo, Sri Lanka, were also used to confirm the identity of specimens. Both wet and dry specimens are deposited in the insect collection of the Department of Zoology, University of Sri Jayewardenepura, Sri Lanka.

RESULTS

Species composition and distribution

Of the 21 ant species in seven subfamilies recorded during the study period (Table 1), the highest proportion belonged to the subfamily Myrmicinae (9 spp.) followed by Formicinae (4 spp.). Only eight species inhabited the house and five of them constructed indoor nests; these species also nested outside the house. *Anoplolepis gracilipes*, *Solenopsis geminata*, *Tapinoma melanocephalum*,

Camponotus sp. 1, *Monomorium* sp. 1 and *Pheidole* sp. 1 were found in all habitats of the home garden (Table 2).

Collection methods and ant species

Of the six methods used, hand collection detected all but one species (*Cerapachys* sp. 1) (Fig. 2). *Aenictus* sp. 1 and *Pachycondyla* sp. 1 were collected only by hand collection. Of the baits

used, fish bait attracted the highest number of species (14 spp.). Winkler extraction of leaf litter yielded a similar number of species, and *Cerapachys* sp. 1 was collected only by this method. Seed baits attracted the fewest species: *Pheidole* sp. 1, *Pheidologeton diversus*, *Meranoplus bicolor*, *Odontomachus haematodus* and *Diacamma rugosum*. Comparatively few ant species were recorded from the pitfall traps.

Table 1. Species composition of ants collected from the home garden and indoors. Given are the subfamily, the species, the number of nests recorded and the nest type.

Subfamily	Species	No. of different nests recorded	Nest type
Aenictinae	<i>Aenictus</i> sp. 1	0	-
Cerapachyinae	<i>Cerapachys</i> sp. 1	3	LG
Dolichoderinae	<i>Tapinoma melanocephalum</i> (Fabricius)	83	I / LG / LT
	<i>Technomyrmex albipes</i> (F. Smith)	116	I / LG
Formicinae	<i>Anoplolepis gracilipes</i> (F. Smith)	0	-
	<i>Camponotus</i> sp. 1	306	S/ BA
	<i>Oecophylla smaragdina</i> (Fabricius)	48	A
	<i>Paratrechina longicornis</i> (Latreille)	27	I / LG
Myrmicinae	<i>Cardiocondyla nuda</i> Emery	4	BA / LG
	<i>Crematogaster</i> sp. 1	18	BA / LG
	<i>Lophomyrmex quadrispinosus</i> (Jerdon)	68	BA / LT
	<i>Meranoplus bicolor</i> Guerin Meneville	52	BA
	<i>Monomorium</i> sp. 1	21	I / BA
	<i>Myrmicaria brunnea</i> Saunders	92	BA
	<i>Pheidole</i> sp. 1	278	BA
	<i>Pheidologeton diversus</i> (Jerdon)	13	BA
	<i>Solenopsis geminata</i> (Fabricius)	42	BA / I
Ponerinae	<i>Diacamma rugosum</i> (Le Guillou)	106	C
	<i>Odontomachus haematodus</i> (Linnaeus)	74	C
	<i>Pachycondyla</i> sp. 1	0	-
Pseudomyrmecinae	<i>Tetraoponera</i> sp. 1	12	LG / A
Total number of nests		1363	

Subterranean nests (S), below- and above-ground nests (BA), above-ground concealed nests (C), arboreal nests (A), lignicolous (LG), lithocolous (LT) and indoor nests (I).

Table 2. Distribution of ant species and number of nests in different habitats of the home garden

Ant species	House	Habitat 1(front garden)	Habitat 2(grassland)	Habitat 3(mixed vegetation)	Habitat 4(footpaths)
<i>Aenictus</i> sp. 1	-	-	-	1	-
<i>Cerapachys</i> sp. 1	-	-	-	3	-
<i>Tapinoma melanocephalum</i>	15	6	16	46	✓
<i>Technomyrmex albipes</i>	22	26	✓	68	-
<i>Anoplolepis gracilipes</i>	✓	✓	✓	✓	✓
<i>Camponotus</i> sp. 1	1	96	47	36	126
<i>Oecophylla smaragdina</i>	-	9	-	39	-
<i>Paratrechina longicornis</i>	10	2	15	-	✓
<i>Cardiocondyla nuda</i>	-	-	-	-	4
<i>Crematogaster</i> sp. 1	-	✓	-	12	6
<i>Lophomyrmex quadrispinosus</i>	-	15	6	-	47
<i>Meranoplus bicolor</i>	-	3	28	?	21
<i>Monomorium</i> sp. 1	14	✓	3	4	?
<i>Myrmecaria brunnea</i>	-	16	ii	73	3
<i>Pheidole</i> sp. 1	✓	46	67	30	135
<i>Pheidologeton diversus</i>	-	-	-	13	-
<i>Solenopsis geminata</i>	✓	5	32	✓	5
<i>Diacamma rugosum</i>	-	11	23	65	7
<i>Odontomachus haematodus</i>	-	7	29	38	✓
<i>Pachycondyla</i> sp. 1	-	-	-	✓	-
<i>Tetraoponera</i> sp. 1	-	12	-	✓	-
Total no. of species	8	16	13	18	14
Total no. of species nesting (no. nests)	5 *(62)	13 *(254)	10 *(266)	12 *(428)	9 *(354)

✓ Species present, - Species absent, * () Number of nests recorded

Nest morphology of ants

Active nests were encountered for 18 ant species. For these, nests were found in all habitats from which the species were recorded (Table 2), but nests of *Aenictus* sp. 1, *Pachycondyla* sp. 1 and *Anoplolepis gracilipes* were not encountered. A total of 1,363 ant nests were encountered during the 15 month study period (Table 1); nest entrances without overlapping debris or structures were presumed to be from separate nests.

Nine ant species (Myrmicinae and Formicinae) constructed subterranean nests with above-ground cone or mound structures surrounding the nest entrance.

In one species of *Camponotus*, two types of nest morphology were encountered. This species usually constructed subterranean nests with a small entrance hole, just large enough for a single ant to squeeze through (Fig. 3). However, it

sometimes constructed crescent-shaped nest mounds about 6 cm in height and a single entrance hole at the centre (Fig. 4). A large number of workers and reproductives were seen emerging during mild rain. Observations on emergence of different castes of ants before and after the rains are shown in Figures 5 and 6 respectively.

The nests of *Myrmecaria brunnea* were massive and prominent. The nest mounds were easily recognizable by their specific wide entrance hole, surrounded by relatively large earthen pellets (Figs. 7 and 8). Their nests remained active for a longer period of time; I have noted one nest for eight years in the same location in the front garden. *Pheidologeton diversus* constructed massive, long-lasting nests in moist loamy soil in shady places, but seldom under stones. This species was regularly observed forming long foraging columns on the ground.

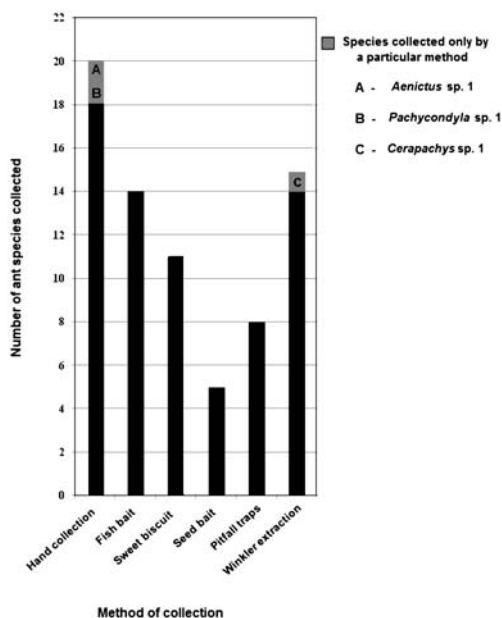


Fig. 2. Number of ant species collected by different methods.

Meranoplus bicolor and *Pheidole* sp. 1 usually constructed their nests in bare areas, away from dense vegetation with prolonged shade. A semicircle or ring of grass seeds or piles of discarded seeds and seed coats were frequently observed near the nest entrance of both species. Following a downpour, if the subterranean granaries became waterlogged, grain was brought up by ants on the first sunny day, spread over the ground around the nest and carefully guarded until the seeds dried. Unlike *Meranoplus bicolor* which constructed solitary nests (Fig. 9), most nests of *Pheidole* sp. 1 had a cluster of small nests scattered on the ground (Fig. 10).

Lophomyrmex quadrispinosus used pure dry sand to construct its nests, choosing warm, dry, exposed spots in hard crusted habitats (e.g., cracks in concrete objects) (Fig. 11). Of the nest types of different ant species observed, a large number of minute entrance holes were present only in this species (Fig. 12).

Nests of both *Cardiocondyla nuda* and *Cerapachys* sp. 1 were inconspicuous in nature.

Cardiocondyla nuda nested in bare ground, and rarely in cavities in decaying logs. *Cerapachys* sp. 1 tended to nest in rotten wood and leaf litter.

The red tropical weaver ant, *Oecophylla smaragdina*, was found to construct its arboreal nests in trees such as *Artocarpus altillius* (breadfruit), *Mangifera indica* (mango), *Citrus acida* (lemon) and *Persea americana* (avocado) (Fig. 13). Nests of *Tetraponera* sp. 1 were observed in hollow twigs and in galls of *Gliricidia* plants. They were occasionally found foraging on the ground, moving very fast.

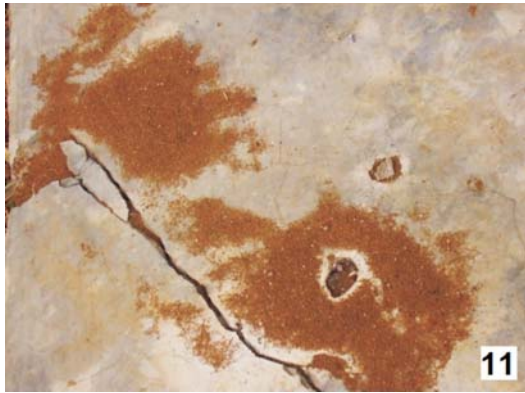
Nests of *Technomyrmex albipes* were found outdoors, in trees and bushes (Fig. 14), and indoors, in crevices of walls and various other objects (Fig. 15). Indoors, they formed distinct, long foraging lines with many workers moving between the nest site and food source. Nests of *Crematogaster* sp. 1 were found in hard crusted soil (Fig. 16) as well as beneath a mat of epiphytes associated with *Pinus* and mango trees.

Tapinoma melanocephalum and *Solenopsis geminata* nested in a variety of habitats, in both open and sunny sites: in bare soil or beneath objects, in rotting logs, loose bark, between rocks and in almost any suitable-sized cavity indoors (Fig. 17). A single nest of *Solenopsis geminata* was found in association with a termite nest in Habitat 3. Nests of *Monomorium* sp. 1 were easily detected due to the presence of a large number of workers foraging in the vicinity. It is a common nuisance species found inside the house. Nests of *Paratrechina longicornis* were found indoors among books and wall cupboards and outside among dead grasses and cavities in detritus.

The ponerines *Diacamma rugosum* and *Odontomachus haematodus* constructed simple terrestrial nests. Usually, their nests had no distinct mound, and were found beneath stones and decaying bark of logs and at the base of large trees (Fig. 18). Many of these terrestrial nests were used only for a short period as the colony kept moving to new sites.

Although it was not possible to locate nests of *Anoplolepis gracilipes*, the ants were abundant and present in the entire study site. Specific details of nests observed of the 17 species of ants during the study period are given in Table 3.





Figs. 3–4. Different nesting habits of *Camponotus* sp.1: 3– A subterranean nest showing only the entrance hole; 4– Crescent-shaped nest showing nest entrance and excavated soil away from the entrance. **Figs. 5–6.** A subterranean nest of *Camponotus* sp.1 showing: 5– The emergence of a few individual ants before the rains; 6– A large number of individuals emerging from the nest after the rains. **Figs. 7–8.** Nests of *Myrmecaria brunnea*: 7– A huge nest showing large entrance hole at the centre of the excavated soil; 8– Partially completed nest located in the footpath. **Fig. 9.** A solitary nest of *Meranoplus bicolor* showing scattered grass seeds around the tumulus. **Fig. 10.** A cluster of *Pheidole* nests in exposed soil showing three entrance holes. **Figs. 11–12.** Nests of *Lophomyrmex quadrispinosus*: 11– Constructed in crevices of hard cement floor; 12– Constructed using sand only. **Fig. 13.** Arboreal nest of *Oecophylla smaragdina* constructed in a lemon tree. **Figs. 14–15.** Nests of *Technomyrmex albipes*: 14– Constructed in association with an herb; 15– Exposed indoor nest constructed on a serving tray showing eggs, pupae and adults. **Fig. 16.** Nest of *Crematogaster* sp.1 with excavated soil in a sparsely weedy patch. **Fig. 17.** Nest of *Solenopsis geminata* constructed in a grass patch in the footpath. **Fig. 18.** Nest of *Diacamma rugosum* constructed at the base of a banana tree.

Table 3. Details of nest morphology of ants in the study site.

Ant species	Nest type	Diameter of nest entrance (mm)	Area of “crater” (cm ²)	Size of soil pellets in entrance hole (mm)	Type of soil used	No. of entrance holes per nest
<i>Cerapachys</i> sp. 1 (n = 3)	LG	6-12	none	-	-	1
<i>Tapinoma melanocephalum</i> (n = 72)	I	5-8	3-7	-	-	1
<i>Technomyrmex albipes</i> (n = 78)	I	7-10	5-8	-	-	1
<i>Camponotus</i> sp. 1 (n = 185)	S	6-10	none	-	clay	1
<i>Camponotus</i> sp. 1 (n = 74)	BA	4-7	56–68	2-3	clay loam	1
<i>Paratrechina longicornis</i> (n = 17)	I	4-6	12-63	1-2	sandy loam	1-2
<i>Cardiocondyla nuda</i> (n = 2)	BA	1-4	3-6	-	-	1
<i>Crematogaster</i> sp. 1 (n= 8)	BA	7-10	67-78	2-3	clay	1
<i>Lophomyrmex quadrispinosus</i> (n = 58)	BA	1-2	314 - 11,315	1-2	sandy	15-20
<i>Meranoplus bicolor</i> (n = 48)	BA	8-12	57-132	2-3	loamy	1
<i>Monomorium</i> sp. 1 (n = 17)	BA	2-6	12-28	1-2	clay loam	1
<i>Myrmecaria brunnea</i> (n = 85)	BA	20-120	157 - 7,857	2-4	silty loam	1-4
<i>Pheidole</i> sp. 1 (n = 247)	BA	6-12	19-28	1-3	clay loam/ sandy	1
<i>Pheidologeton diversus</i> (n = 13)	BA	15-50	177-347	2-4	loamy	1-3
<i>Solenopsis geminata</i> (n = 32)	BA	4-20	13-452	1-3	sandy loam	2-25
<i>Diacamma rugosum</i> (n = 52)	C	10-25	78-5,028	1-3	sandy loam	1-6
<i>Odontomachus haematodus</i> (n = 65)	C	8-15	58-2,560	-	-	1-7
<i>Tetraponera</i> sp. 1 (n = 8)	LG	5-15	none	-	-	1-3

n = Number of nests measured. Nest types: Subterranean or below-ground nests (S), below- and above-ground nests (BA), above-ground concealed nests (C), arboreal nests (A), lignicolous (LG), lithocolous (LT), and indoor nests (I).

Density of ant nests

When the density of ant nests within 10 m² was considered, Habitat 3 with undisturbed tall trees had the highest mean density of 2.85 nests/m²,

followed by footpaths (Habitat 4: 2.36 nests/m²). The lowest nest density was found indoors (0.41 nests/m²). A comparison of nesting densities among different habitats during the study period is illustrated in Fig. 19.

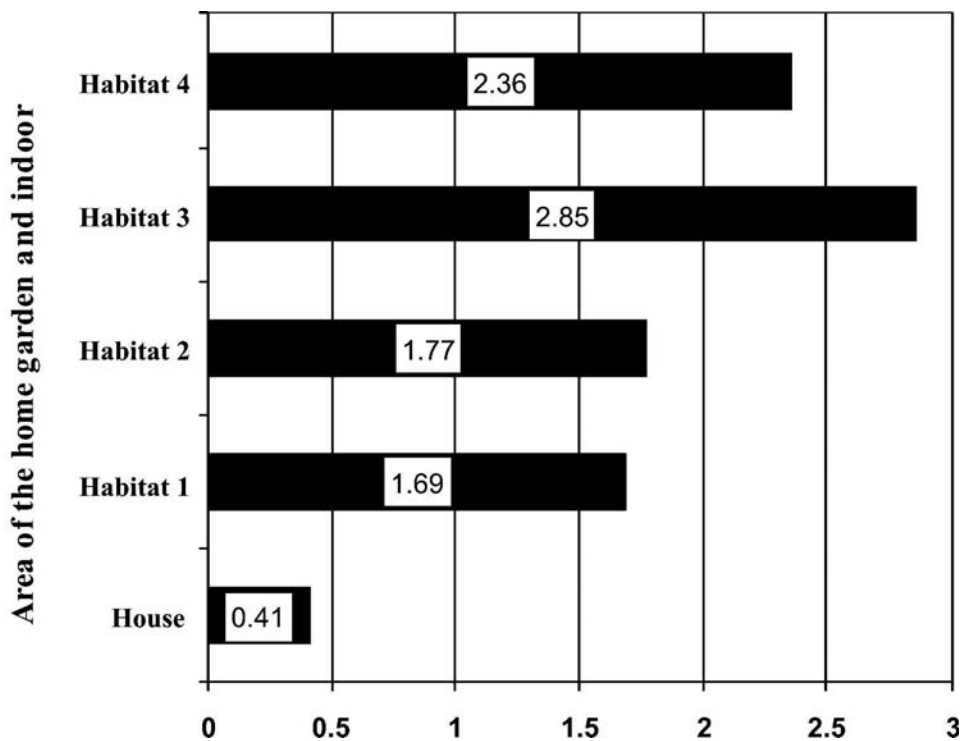


Fig. 19. Nest densities of ants in different habitats of the home garden and indoors during 15-month study period.

DISCUSSION

The present study recorded 21 genera of ants, one-third of the ant genera recorded for Sri Lanka (Dias 2002). The highest nesting density (almost 3 nests/m²) was in Habitat 3, which had the highest variety of microhabitats including trees, epiphytes, leaf litter, decaying logs and stones. *Pheidologeton diversus*, *Aenictus* sp. 1, *Cerapachys* sp. 1 and *Pachycondola* sp. 1 were confined to Habitat 3, and generally seen foraging in dense leaf litter. Most species in these genera are specialized predators (Agosti *et al.* 2000), which feed on a restricted set of arthropods; it is possible they were limited by distribution of food sources.

Rapid reconstruction of nests was observed about a week after a fire, especially by ants of the genera *Camponotus*, *Pheidole* and *Lophomyrmex*, and they reoccupied the area successfully after being eliminated. However, the land was first occupied by predatory ant species such as *Diacamma rugosum*, *Odontomachus haematodus* and the invasive pest ant *Solenopsis geminata*.

Unlike the temporary nests of other species, high longevity in nests of *Myrmecaria brunnea* was observed. Their nests sometimes remained active for several years; I noted one live nest active for eight years in the front garden of the study site, and a similar nest, occupied by the same species in a soil cavity made by replacing an

old lemon tree, was observed in a neighbouring home garden for about 25 years. Although the nest entrance was swept out regularly by humans and the nest entrance-hole filled and packed with soil, they rebuilt it in the same location. Presumably, the disadvantage of frequent disturbance continued to be outweighed by the site's favourable ecological conditions; in addition, the nest may have spread deep underground such that only a small part of it was disturbed.

Among the total of 1,363 ant nests encountered during the study period, the number of indoor nests (62) was comparatively low. Indoor nesting sites are usually associated with books, clothes, furniture and other household items which are frequently subject to disturbance. Thus, all 18 nesting species of ants nested outdoors while only five nested indoors. These included *Tapinoma melanocephalum*, *Technomyrmex albipes*, *Paratrechina longicornis* and *Monomorium* sp. 1 which are usually identified as invasive pest ant species common to many household environments. Only a single nest of *Camponotus* sp. 1, a subterranean nest with a small cryptic hole in the ground, was found indoors. Most such nests were constructed outdoors and the species appears to be an opportunist that moves nests frequently. Other species such as *Solenopsis geminata* and *Pheidole* sp.1 were common indoor visitors but nested outdoors, where abundant sunlight was received. They seemed to come indoors only for food.

All the indoor-nesting ant species select damp, shady and hidden locations for their nesting sites. Such ecological differences are likely to influence the selection of nesting site by different ant species. Although the internal environment of a house changes rapidly, these ants are highly adapted to move their nests suddenly, and can quickly build new nests in different indoor locations.

Ants were found to construct nests in a variety of soil types from hard clay to loam to pure sand. For example, while *Lophomyrmex quadrispinosus* nested only in pure sand, *Pheidole* sp. 1 nested in a wide range of soil types including clay, loam or sand. Further work would

be required to determine any physiological and anatomical adaptations to these substrates.

Ants differ in external nest morphology, both between and within species. The shape of a nest is in part determined by the way ants deposit the excavated soil particles. Further work in different habitats with differing soil, vegetation and climatic conditions is needed to test the consistency and flexibility of nesting habits reported here.

ACKNOWLEDGEMENTS

I am grateful to Prof. J.P. Edirisinghe, Head of the Department of Zoology at the University of Peradeniya for her comments on the manuscript. The Department of Zoology, University of Sri Jayewardenepura is acknowledged for providing microscopic facilities for identification of ants.

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