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An Assessment of Pedoturbation by two Species of Mound-building Ants, *Camponotus intrepidus* (Kirby) and *Iridomyrmex purpureus* (F. Smith)

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Abstract

Details of the size, structure and occurrence of *Camponotus intrepidus* nests and the size, composition and source of the mound cover on *Iridomyrmex purpureus* nests are reported from several areas of eastern New South Wales. Both species are common, and construct large mounds of mixed topsoil and subsoil with surface covers, which appear to protect the mound from rainsplash erosion. *Camponotus* thatches the mound with charcoal, leaves and twigs; *Iridomyrmex* covers the mound in granules of inorganic or organic material that are sufficiently large to absorb most raindrop impact energy. This material is collected from the surface and carried 10-15 m to the nest. Rainsplash erosion protection is probably a factor contributing to nest longevity, which may be as much as 100 years for *Iridomyrmex*. It is concluded that, despite the impressive size of the nests and the selective use of materials, neither species is very significant in terms of soil mixing when compared with the smaller, more common ant *Aphaenogaster longiceps*.

Introduction

The role of ants in soil formation has been recognized by a number of investigators (e.g. Branner 1896; Baxter and Hole 1967; Mandel and Sorenson 1982), who have shown that ants undertake various soil-altering actions which include depositing subsoil on the surface, reducing the soil bulk density, increasing concentrations of organic matter, influencing nutrient cycles, and impeding soil horizonation through the process of pedoturbation (Hole 1961). Within some areas of the Sydney Basin, Humphreys (1981) and Humphreys and Mitchell (1983) have shown that the funnel ant, *Aphaenogaster longiceps* (F. Smith), is a very important agent of soil turnover.

The only other Australian genus which has been examined in this context is the meat ant *Iridomyrmex*, a complex group of 10 sibling species (Greenslade and Halliday 1982), not all of which are yet described. *Iridomyrmex purpureus* is the most widely distributed species and only one form, *I. purpureus* sensu stricto, is recognized in eastern New SouthWales. Most of the published studies related to this form, and it was also the subject of our research. Ettershank (1968) carried out an investigation to establish the three-dimensional structure of the meat-ant nest, and Greenslade (1974) examined the relationships of the meat ant with soils in South Australia. He reported that soil-turnover rates by this species were very low, and

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that there was virtually no mixing of soil horizons in the nest. This result, combined with the reported longevity of nests (Anon. 1956), suggested that this species was not a significant agent of pedoturbation.

Both the meat ant and another species, *Camponotus intrepidus*, are common on the sandstone landscapes of the Sydney Basin. In both cases their nests are constructed in and beneath conspicuous mounds of soil which, in the case of the meat ant, are capped by a fine gravel layer and, in the case of *Camponotus*, by a thatch of organic debris. Although originally described over 160 years ago by Kirby (1818), the present taxonomic status of *Camponotus intrepidus* is uncertain, and we have been unable to find any subsequent substantive literature on the species.

As part of an ongoing project assessing the relative importance of all forms of physical turnover and erosion in soil genesis, we have examined the mounds and nests of both species to determine their significance as agents of pedoturbation in the warm temperate environments of the Sydney Basin.

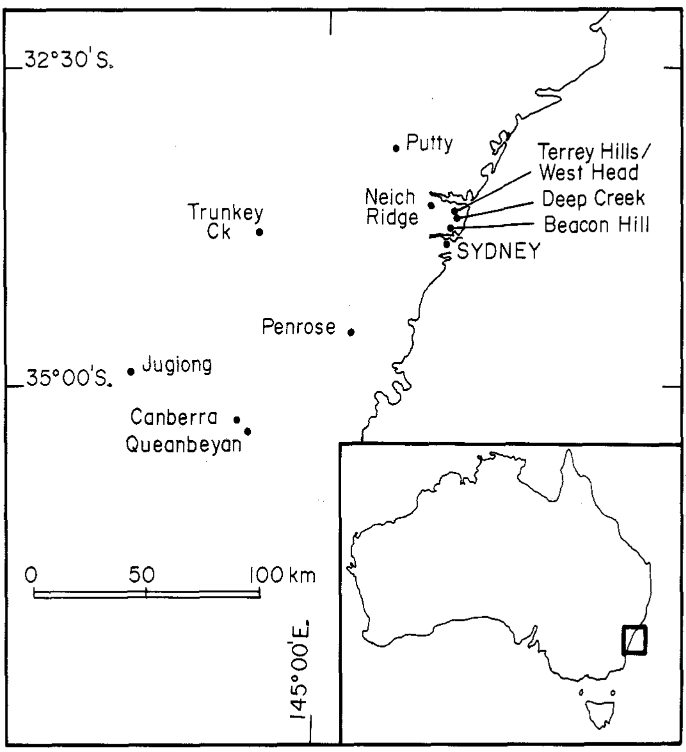


Fig. 1. General location of study areas and sample sites.

Study Areas and Methods

Camponotus *Study*

The study of *C. intrepidus* nests was concentrated on a 2·24 ha plot at Beacon Hill, 14 km north of Sydney, at an altitude of 134 m (Fig. 1).

This Hawkesbury Sandstone site had a 10° slope and yellow podzolic soils (Stace *et al.* 1968), with Northcote (1971) principal profile forms of Dy 5·51 or Dy 5·61. Sandstone outcrops were common, and in some places bedrock was covered by a shallow, sandy soil, equivalent to the A horizon of the podzolics. This profile was typically 20–30 cm deep and was classified as a siliceous sand or Uc 4·11.

The vegetation was a low, open woodland, dominated by *Angophora costata* and *Eucalyptus piperita*, with a disturbed shrub understory of *Banksia serrata*, *Acacia botrycephala*, *Grevillea punicea*, *G. buxifolia*, *Darwinia fascicularis*, *Hakea bakerana*, *H. gibbosa*, *Dillwynia retorta* and *Boronia ledifolia*.

Within the study area 12 ant mounds were located and their aboveground dimensions noted. Two nests (13 and 14) outside the study area were also examined, and data from these are included in the relevant tables. Ants collected from the nests were identified as *Camponotus intrepidus* by Dr M. Fletcher, New South Wales Department of Agriculture, and voucher specimens were lodged with the Australian National Insect Collection in Canberra; Dr R.W. Taylor confirmed the species identification.

A series of soil pits was excavated in the vicinity of the mounds, and nest 1 was sectioned to determine its general structure. Eight undisturbed soil samples were taken in Kubiena tins from a vertical face across the centre of this nest, and these were subjected to binocular microscope examination of soil fabric. Duplicate homogenized samples from these tins were separated into coarse sand, fine sand and silt plus clay fractions using the settling technique of Day (1965). Gravimetric soil-moisture determinations were made from various depths within several nests, and compared with the adjacent soil on three different occasions after rainfall.

In order to measure total nest volume and nest shape, three casts were made. The first of these, on nest 5, used dental plaster, but this proved to be too weak to withstand excavation intact. Subsequent casts of nests 13 and 14 were made with a portland cement slurry to which 3% calcium chloride had been added to hasten setting and cure. Both casts were excavated with only slight damage and reassembled on a simple frame using rapid-cure epoxy resin. The most successful excavation technique was to wash the cast out of the soil with a hose connected to the domestic water supply.

Iridomyrmex *Study*

The field study of *I. purpureus* nests involved two independent collections and analyses. One of us (G.S.H.) examined 18 nests (set 1) on Hawkesbury Sandstone ridge tops in three separate areas. Six were in a *Eucalyptus gummifera–Angophora hispida* association at Neich Ridge, 41 km north-west of Sydney; 6 in a *Eucalyptus gummifera–Banksia serrata* association at Deep Creek, 21 km north of Sydney; and 6 in a *Eucalyptus gummifera–E. haemostoma* association on the West Head road, 27 km north of Sydney. In the second study, another of us (P.B.M.) sampled 46 nests (set 2); 25 adjacent to roads in the vicinity of Terrey Hills, 22 km north of Sydney, also on Hawkesbury Sandstone ridge tops; 5 on porphyry at Canberra; 5 on metasediments at Queanbeyan; 5 on granite at Jugiong; 2 on basalt at Trunkey; 2 on sandstone at Putty; 2 on sandstone and nodular ironstone at Penrose (Fig. 1).

For all the nests our main interest was in the nature of the mound cover, and particle-size analyses were conducted by sieving ($\frac{1}{2}\phi$ intervals for set 1, $\frac{1}{4}\phi$ for set 2). Use of the ϕ scale ($-\log_2$(particle diam. in mm)) enabled calculation of standard sedimentological grain size statistics using the formulae of Folk (1974).

Grain mineralogy was determined under a binocular microscope, and the proportion of the various components assessed by direct counting (minimum of 239 grains per mound for set 1; 500 for set 2).

Results

Camponotus *Study*

Camponotus intrepidus is a large ant with polymorphic workers, the majors reaching 20 mm in length. No ant activity was observed on the surface by day except when nests were disturbed. Nests were repaired by the ants at night, and it seems that the species is nocturnal.

Nests were partly shaded by overhanging shrubs and trees and the above-ground part of each nest was an earthen mound, constructed around two or three clumps of grass or sedges and crudely thatched with leaves, twigs and charcoal fragments worked into the mineral soil on the mound surface (Fig. 2). The sides of the mound were sometimes fluted, and in such cases the debris cover was incomplete. During the study period (August to January) there were no visible entrance holes on any mound and, in order to make the nest casts, it was necessary to lift off a 1 cm thick

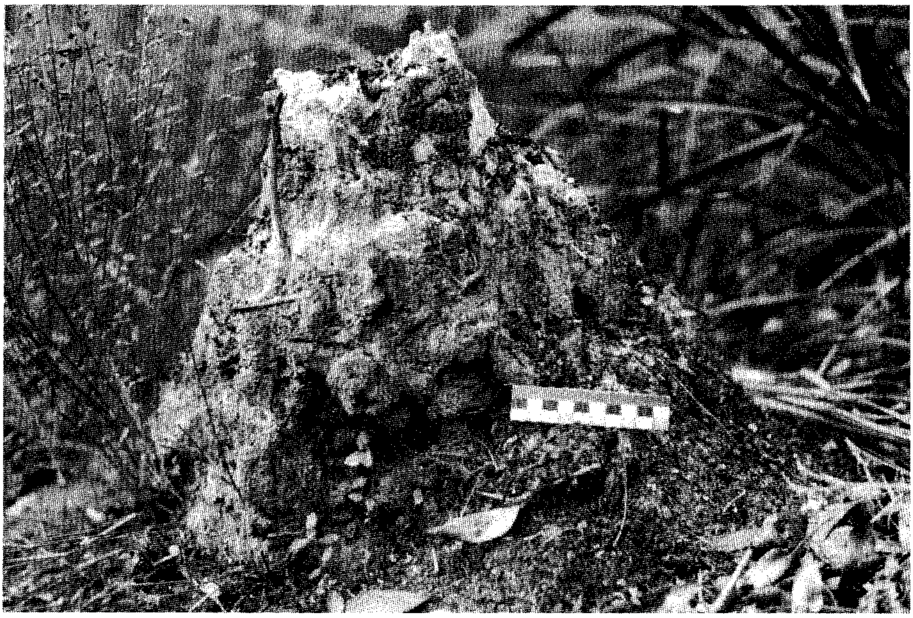


Fig. 2. A typical *Camponotus intrepidus* nest photographed in late winter. Much of the mound thatch has been washed off, and the mound is fluted by rainsplash. Scale, 10 cm long.

Table 1. Surface dimensions of the *Camponotus intrepidus* mounds at Beacon Hill, N.S.W.

Nest No.	Plan shape	Length (cm)	Width (cm)	Height (cm)
1	elliptical	190	75	25
2	elliptical	60	55	25
3	elliptical	17	13	12
4	elliptical	45	35	22
5	round	—	Not recorded	—
6	elliptical	42	25	15
7	round	42	42	30
8	round	43	40	10
9	round	60	56	16
10	round	30	28	18
11	elliptical	65	50	33
12	elliptical	30	22	28
13	elliptical	42	30	11
14	round	44	40	20
		Av. 55	Av. 39	Av. 20·4

surface crust from the mound to gain access to the galleries. The mounds varied in ground-surface area from 0·05 to 1·19 m^2, were commonly elliptical, and rather peaked, with a mean height of 20·4 cm (Table 1). Mounds occupied only 0·01% of the study plot.

The colour of the mineral soil in most mounds indicated that at least some of the soil was derived from the B horizon of the yellow podzolic soil on the site. These soils may be typified by the following brief description:

A_0, 0–2 cm	Undecomposed leaf litter, twigs and charcoal fragments, sometimes interspersed with clean, single-grained sands. Sharp to:
A_1, 2–10 cm pH 5·0	Loamy sand to sandy loam, brown to brownish black 10YR3/2 m to 4/2 m, single-grained, bound by root hairs and fungal hyphae. Clear wavy to:
A_2, 10–25 cm pH 4·5	(This horizon not always present.) Sandy loam, dull yellowish brown 10YR5/3 m, apedal single-grain, fine sands. Roots common, clear wavy to:
B_2, 25–55 cm pH 4·5	Sandy clay loam to light clay, dull yellow 2·5Y6/4 m, usually mottled, apedal massive with a dense earthy fabric, roots sparse, gradual boundary to weathered sandstone or grey clay from weathered shale.

Excavation of nest 1 revealed that most ant galleries were located in the mound and in the A horizon of the soil. A few galleries extended to the C horizon of grey plastic clay at a maximum depth of 90 cm, but the degree of soil mixing was not so intense as to destroy the visible soil horizonation below 25 cm. Fig. 3 shows a central section through this nest and the position of the Kubiena tin samples. Grain-

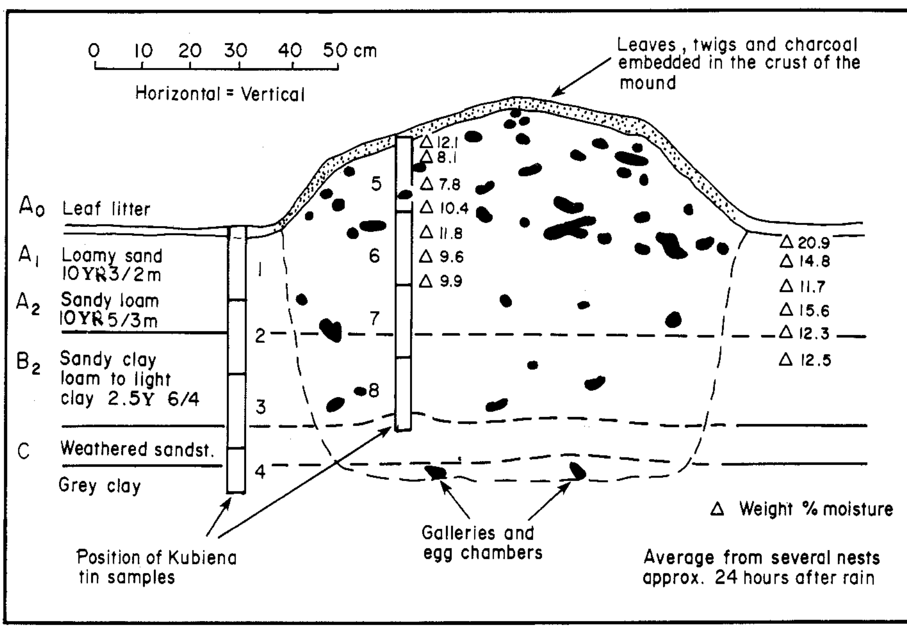


Fig. 3. Vertical section through *Camponotus intrepidus* nest 1, showing the relationship of the mound and galleries to the soil.

size analyses of these samples showed an increase in the proportion of silt plus clay in the mound compared with the adjacent A horizon, and a corresponding decrease in the coarse sand fraction (Table 2).

The sectioning technique did not give a clear view of the entire nest structure, but did indicate that the galleries interconnected only within the mound. Below this there were several independent open spirals, each serving 8–12 chambers.

Examination of the Kubiena tins revealed more details of the nest structure. The mound was seen to be composed of thoroughly reworked soil, consisting of 5–8 mm clumps of B horizon clay intermixed with A horizon sands and coarse organic debris. Galleries within the mound had 'glazed' walls 2–3 mm thick of a colour darker than the mound itself. Macerated fine organic matter (leaves, rootlets) were incorporated in this glaze and were visually estimated to comprise 20% of the wall material. Termite galleries and the nest of a small black undetermined ant sp. shared the mound, but neither of these nests connected with *Camponotus* galleries. With increased depth, the gallery wall glaze thinned to between 0·5 and 2 mm, and the colour became similar to the enclosing soil. Fine leaf material was used in the lining even at the base of the nest, and occasional large quartz grains and root tips extended through the lining into the galleries. The wall lining of chambers averaged 5 mm thick.

Table 2. Particle size analysis of *Camponotus intrepidus* mounds and adjacent soil at Beacon Hill, N.S.W.

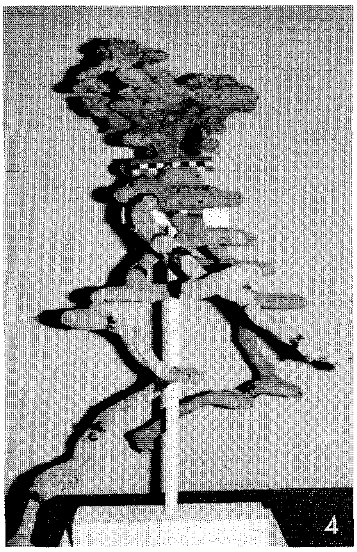
Sample No. (Fig. 2)	Coarse sand 2·0–0·2 mm	*Weight (%)* Fine sand 0·2–0·02 mm	Silt plus clay <0·02 mm
1 (A_1, of soil)	36·9	38·6	24·5
2	3·2	73·1	23·7
3	1·4	33·3	65·3
4	0·2	15·4	84·4
5 (mound)	12·3	43·7	44·0
6	7·9	62·4	29·7
7	4·8	58·6	36·6
8	0·6	16·6	82·8

Table 3. Comparative statistics of the three *Camponotus intrepidus* nest casts from Beacon Hill, N.S.W.

Nest No.	Total nest volume (cm^3)	Maximum nest depth from the ground surface (cm)	Gallery diameters (mm)	No. of chambers
5	10 825	Approx. 90	13–25, Mean 18	68
13	2 959	52	13–27, Mean 20	31
14	4 468	17	13–23, Mean 18	Approx. 40

Total nest volumes, the number of chambers and the diameter of galleries were obtained from the three nest casts (Table 3), most galleries were circular to slightly elliptical, and in nest 13 a definite decrease in diameter with depth was observed which may be a common feature.

Of the four nests examined in detail, 5 and 13 were similar in structure to 1. Fig. 4 shows the cast of nest 13, which had three spiral arms extending to 52 cm depth in the B horizon of the soil. Fig. 5 shows the cast of nest 14, which was quite unlike the other nests. All the galleries and chambers were densely packed together, yet still separated by gallery walls 2–3 mm thick, except in the upper mound where



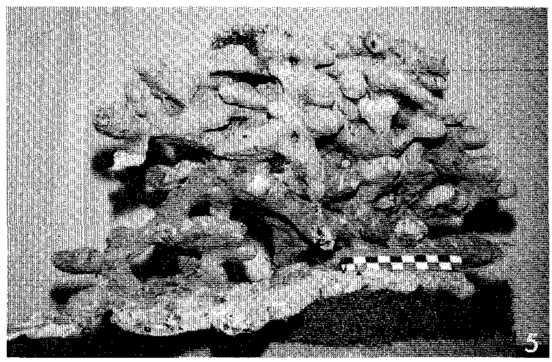


Fig. 4. Internal cast of *Camponotus intrepidus* nest 13. Original mound height 11 cm, maximum depth of gallery penetration 52 cm. This spiral form seems to be typical. Scale, 10 cm long.

Fig. 5. Internal cast of *Camponotus intrepidus* nest 14. Original mound height 20 cm, maximum depth of gallery penetration 17 cm. This unusual nest was constructed in shallow soil and confined by bedrock. Scale, 10 cm long.

there was some interconnection. This nest was constructed in a siliceous sand (Uc 5·11) above sandstone bedrock at 17 cm depth. Immediately above the bedrock, a discontinuous stone line of iron-rich sandstone pebbles occurred, and the lower galleries were excavated between the pebbles, which in places protruded through the gallery walls.

During excavation the mounds and upper parts of the nests were always seen to be drier than the adjacent soils. Soil moisture was measured on three occasions approximately 24 h after rain, and the results confirmed this observation (Fig. 3).

Iridomyrmex *Study*

Our examination of *Iridomyrmex* nests has not been as comprehensive as those of *Camponotus.* Excavation of several nests has confirmed the general structural details noted by Ettershank (1968) and Greenslade (1974). These authors noted that the number of entrance holes varied seasonally, and each hole served a single set of galleries and chambers linked by a vertical shaft. Most galleries were clustered in the upper 30 cm of soil and mound, but some extended well into the subsoil. The mounds studied in set 1 were circular or elliptical, with mean dimensions of

160 by 125 cm and 23 cm high. They varied in size from 65 by 40 cm to 270 by 230 cm and in height from 5 to 42 cm. Corresponding size variation in set 2 was from 46 cm diameter to 244 by 107 cm. Heights were not recorded for these mounds and the mean size was 146 by 102 cm. These sizes are similar to those reported by others (e.g. Greaves and Hughes 1964), except that the mounds of set 1 appeared to be a little higher than usual. Whether this is a valid observation or merely an artifact of sampling obvious mounds, rather than all mounds, we cannot say.

Table 4. Grain size statistics and composition of mound cover on *Iridomyrmex purpureus* nests, set 1, Hawkesbury Sandstone sites
(Statistics terminology of Folk 1974)

Nest No.	Graphic mean, ϕ	Graphic s.d.	Graphic skewness	Graphic kurtosis	Number (%) Composition: Quartz	Sandstone	Blue Metal	Charcoal	Twigs etc.
				Neich Ridge					
1	−1·157	0·501	+0·071	0·861	9·9	69·6	0	13·5	7·0
2	−1·146	0·463	−0·037	0·990	38·9	38·2	0	19·7	3·2
3	−1·125	0·482	+0·044	0·941	38·7	33·6	0	19·6	8·1
4	−1·167	0·510	−0·102	0·854	55·7	38·1	0	4·4	1·8
5	−1·501	0·418	+0·294	0·939	2·5	93·9	0	0·9	2·7
6	−1·342	0·451	+0·100	0·932	4·8	70·6	0	11·6	13·0
				Deep Creek					
1	−1·503	0·418	+0·278	0·837	2·6	84·9	0	11·0	1·5
2	−1·321	0·457	+0·162	0·880	20·3	66·4	0	6·1	7·2
3	−1·388	0·388	+0·033	0·992	0·6	92·1	0	0	7·3
4	−1·459	0·412	+0·179	0·914	26·1	69·7	0	0	4·2
5	−1·405	0·389	+0·225	1·208	16·1	81·3	0	0	2·6
6	−1·471	0·511	+0·342	1·047	4·0	67·2	0	0	28·8
				West Head					
1	−1·371	0·410	+0·092	0·924	7·5	56·6	33·9	0	2·0
2	−1·246	0·342	−0·030	1·255	3·9	52·0	44·1	0	0
3	−1·454	0·470	+0·141	0·918	10·9	66·0	0	0	23·1
4	−1·367	0·370	−0·028	1·004	7·5	39·8	50·1	0	2·6
5	−1·321	0·431	+0·118	1·055	5·4	81·4	9·2	0	4·0
6	−1·384	0·366	+0·012	1·015	10·4	35·5	52·8	0	1·3
Mean	−1·340	0·433	+0·105	0·976					
Range					1–56	34–94	0–53	0–20	0–29

Nest distribution was related to open ground, and nests were common along road verges in the woodland areas of the Hawkesbury Sandstone terrain. This distribution did not appear to be related to soil type, and we have seen mean-ant nests on a range of profiles including the following: Uc 1·22, Uc 4·21, Uc 5·22, Um 5·51, Uf 6·32, Dy 6·32, Dy 2·21, Dy 3·32 and Dg 1·41. The nature of the mound cover, however, varied considerably with nest location.

Most authors have commented on this mound cover, or 'decoration', and several noted that, where inorganic material of the right size was scarce or absent, the mounds were covered with organic materials or even soil crumbs of similar size (e.g. Greaves 1939; Ducan-Weatherley 1953; Ettershank 1968). The presence of these organic components demonstrates that at least part of the mound cover was collected from the surface rather than during excavation of the nest. The literature is not clear on this point, and we have attempted to resolve it by analysing the mound cover in more detail.

The composition of the mound cover and the size parameters of the grains (terminology of Folk 1974) from the nests of set 1 are presented in Table 4. The material comprised coarse sand and fine gravel which were well-sorted, fine-skewed, and mesokurtic. The overall mean size was $-1 \cdot 34\phi$ or $2 \cdot 5$ mm, and the range of individual means $-1 \cdot 13$ to $-1 \cdot 50\phi$, or $2 \cdot 2$–$2 \cdot 8$ mm. The most common components of the mound cover were quartz grains, sandstone fragments, charcoal, twigs, eucalyptus buds or fruit, and miscellaneous materials such as 'blue metal' aggregate, bitumen particles from sealed road surfaces, and fragments of glass from car windscreens.

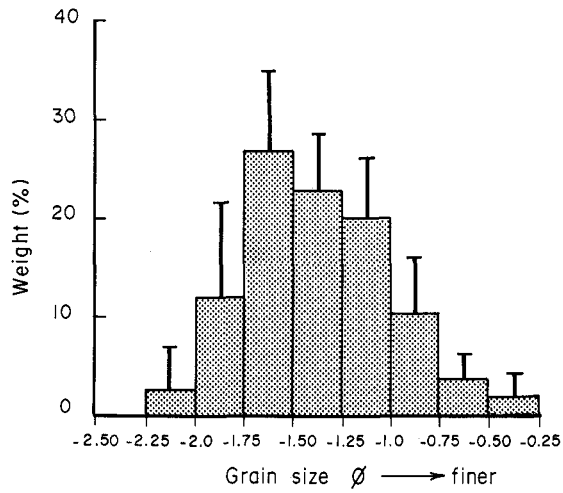


Fig. 6. Grain-size histogram for the mound cover from 25 *Iridomyrmex purpureus* nests in eastern New South Wales (set 2). Error bars represent +1 s.d. Folk graphic mean, $-1 \cdot 39\phi$, equivalent to $2 \cdot 6$ mm diameter.

The results of particle size analyses for 25 samples from set 2 are presented in Fig. 6. The mean grain-size for these samples was $-1 \cdot 39\phi$ or $2 \cdot 6$ mm; the modal size was $-1 \cdot 63\phi$ or $3 \cdot 1$ mm. The range of mean sizes for individual nests, especially those on the Hawkesbury Sandstone, was rather larger than might have been expected. However, this difference could be accounted for by the variation in composition of the mound cover. Mounds with a smaller mean grain-size than the overall mean usually included a higher proportion of fragile materials (charcoal and soil crumbs) which tended to break up during sieving. Mounds with a larger mean grain-size included a high proportion of linear organic fragments (twigs) that were retained on a sieve with a mesh coarser than their minimum diameter. In both cases such samples came from areas where there was little coarse mineral material available in the vicinity of the nests. The most extreme example was a nest on a clay soil derived from basalt at Trunkey. The mound cover of this nest comprised 85% twigs, 10% large superphosphate pellets and 5% basalt fragments (number %, based on grain counts), with a mean grain-size of $3 \cdot 2$ mm. All the mean sizes recorded in our study were larger than those reported by Greenslade (1974). This probably does not reflect a real difference in particle size so much as the difference in techniques used for sampling and size analysis. To determine the distance over which gravel fragments were carried by ants, 21 mounds in the Terrey Hills area (part of set 2) were sampled at varying distances from a sealed road, and the proportion of blue metal from the seal aggregate measured by grain counts. These results are presented in Fig. 7, where it may be seen that mounds located more than 10–15 m from the edge of the road seal contain less than 10% of blue metal, and the proportion increases steeply for mounds closer to the aggregate source. The same analysis was conducted on five mounds from the West Head road (part of set 1). These results are also plotted on Fig. 7. Both sets of data are consistent.

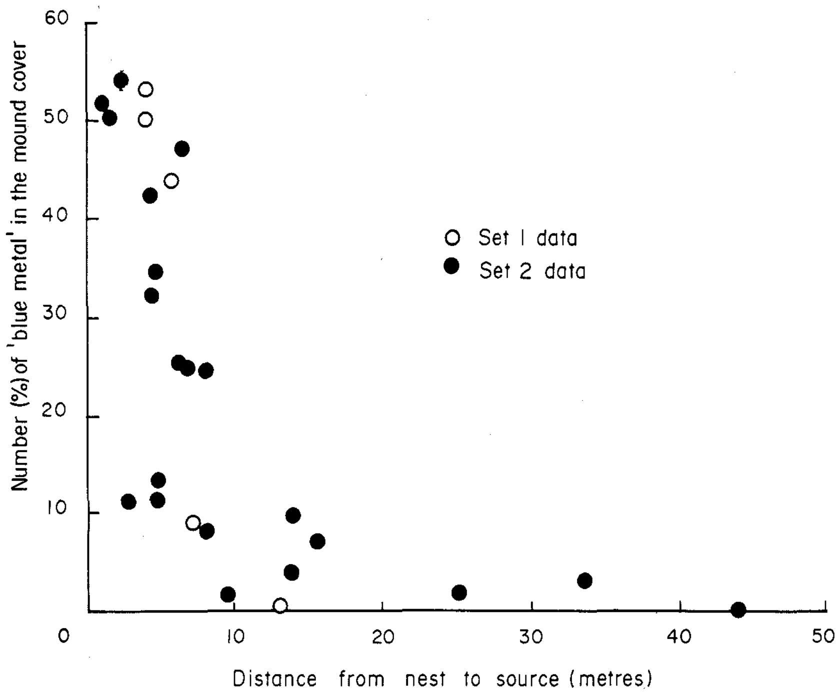


Fig. 7. Proportion of igenous rock fragments ('blue metal') derived from road aggregate found on *Iridomyrmex purpureus* mounds at various distances from the road edge. Terrey Hills and West Head Road, N.S.W.

Discussion

The nests of both species have several common features. Both appear to be common on disclimax sites where the natural vegetation has been damaged by fire or removed. Both construct mounds from excavated soil, both cover the mounds with a protective layer of debris, and both have a similar gallery structure. There are also significant differences. Our observations suggest that *Camponotus* is more tolerant of shaded conditions than *Iridomyrmex*, and this may also apply to other species in the group. Both Ettershank (1968) and Greenslade (1974) noted that overshadowed meat-ant colonies lose vigour and may be invaded by *Camponotus 'consobrinus'* (Erichson).

The nature of the mound cover differs between the species. On *Camponotus* mounds the debris is a thatch of organic material anchored to the soil, which appears to protect the mound from rainsplash erosion. This debris will decay, and must be renewed by the ants as long as the nest is occupied. The duration of our observations was not sufficient to determine whether any seasonal pattern of thatch renewal occurred, but the common occurrence of slightly eroded mounds at the end of winter suggests that such a pattern may exist. Activity by *Camponotus* during the late winter and spring to early summer appeared to be fairly low, and the absence of visible nest openings was puzzling.

The composition of the *Iridomyrmex* mound cover is a function of the relative availability of materials of the appropriate size within 10–15 m of the nest. We have often observed ants carrying coarse particles to the nest from the adjacent surface. The propostion that all these coarse particles are derived from the nest excavation, as suggested by many early authors, is untenable. In none of the nests that we examined was the coarse fraction of the soil sufficient to account for any more than 5–10% of the mound gravel, and the common occurrence of materials exclusive to the surface, including bitumen fragments, glass, and superphosphate, confirms this view.

Several suggestions have been made in the literature as to the function of the *Iridomyrmex* mound cover. These fall into three groups: modifications of the nest microclimate; identification of a behavioural boundary; and protection of the mound from rainsplash erosion.

In our opinion rainsplash erosion protection is the most important role, especially since these nests are all constructed on open sites. Laboratory studies by Mazurak and Mosher (1968) of the rainsplash mechanism in relation to particle size and rainfall intensity have shown that mineral particles larger than 2·36 mm diameter are rarely moved, and average drops are effectively absorbed within the pore spaces. The mean grain-size of the *Iridomyrmex* mound-gravels reported here is well above this figure, and relatively little gravel movement could be expected under most rainfall conditions. Under more intense storms some gravel movement might occur, and larger mounds often have a low flanking apron of gravel and fine sand deposited around their base. Gravel renewal must be a constant task for the *Iridomyrmex* colony, just as thatch renewal is for *Camponotus.* Immediately beneath the gravel cover a crusted soil surface develops on the mound and effectively waterproofs the nest. In some nests several layers of gravel are apparent in the mound, having accumulated during expansion of the colony and growth of the nest.

The possible erosion-protection devices used by both species — thatching and the development of a lag gravel surface — are also known to be used by other species. For example, the mounds of *Camponotus* are very similar to several species of bulldog ant, *Myrmecia,* also common in the Sydney Basin, and the mounds of *Iridomyrmex* are almost identical to those built by species of *Pogonomyrmex* and *Formica* in the western United States, reported by Scott (1951) and Mandel and Sorenson (1982). Erosion protection is probably a major factor in contributing to the longevity of such mounds. In a report of the work of Greaves (Anon. 1965), there was described a colony of *Iridomyrmex* near Canberra that was known to be at least 70 years old, and Greenslade (1974) suggested that mound ages of 100 years were quite possible. Owing to the decay of the organic thatch, *Camponotus* mounds are not likely to last as long as these reported *Iridomyrmex* mounds if the colony dies out at any time. No data are available on *Camponotus* mound age, but one of us (P.B.M.) has been aware of several individual mounds near Sydney for more than 6 years, and these have not shown any obvious change in form during that time. We conclude from this very limited observation that mound longevity is likely to be some tens of years.

The internal structure and volumes of the nests of both species are comparable, with the maximum recorded volume being 11 l. for *Camponotus* (nest 5) and 39·4 l. for an *Iridomyrmex* nest (Greenslade 1974), the latter nest being occupied by a weak colony and having only 10 entrance holes, so a proportion of the galleries was probably unoccupied. If Ettershank's (1968) data of six entrance holes leading to galleries with a total volume of 5 l. are accepted as a norm, it can be calculated that the extremely large nest originally described by Greaves (1939) with 1061 openings could have had a volume of about 800 l. The more typical nest, however, has 24 entrance holes (Greaves and Hughes 1974), which would represent a volume of about 20 l. Too few data are available to be more specific than this, but the indications are that *I. purpureus* move at least twice as much soil in nest construction as do *C. intrepidus*.

Table 5. Comparative data for species involved in soil turnover in the Sydney Basin
See text and Humphreys and Mitchell (1983) for details

	Iridomyrmex purpureus	*Camponotus intrepidus*	*Aphaenogaster longiceps*	Lyrebirds	Earthworms	Treefall	Cicadas
Typical size of disturbed area	150 by 115 cm 10–30 cm high	55 by 39 cm 20·4 cm high	15 cm diam. 5 cm high	Extensive surface feeding >100 m^2	2 cm diam. 1 cm high	1–2 m diam. 10–50 cm deep	3 cm diam.
Longevity of disturbed site	Tens of years	>6 years	weeks	weeks to years	days	<15 years	weeks
Soil disturbance rate (g/m^2/year)	Not determined	<5	570–841	4470	133	19–134	3-20

Our observations and the published data on meat-ant nests all show that galleries are concentrated in the upper 20–30 cm of the mounds and topsoil. Gallery penetration does occur to greater depths, but in all cases this is not enough to destroy visible soil horizonation below the A_1, although finer soil particles are moved to the mound from the subsoil.

Since there was no visible change in the surface form of the nests examined during the period of this study, it is not possible to calculate any rates of soil turnover by either *Camponotus* or *Iridomyrmex*. However, their relative importance may be gauged by calculating the total weight of soil moved to the surface by the 12 *Camponotus* mounds on the study plot. Assuming that the average measured volume of nests 5, 13 and 14 was representative of all the nests, and since the average topsoil density was 1·5 g/cm^3, the total weight of soil in the mounds was about 50 kg/ha or the equivalent of 5 g/m^2. Even if all the mounds were formed in one year (which was certainly not the case), this rate of mounding is minute in comparison with other turnover data reported by Humphreys and Mitchell (1983) from the same environment and summarized in Table 5. Since *Iridomyrmex* mounds are known to have longevities of many years, we conclude that *Iridomyrmex* is also unimportant as an agent of pedoturbation in this environment. This conclusion confirms the view of Greenslade (1974) from his studies in South Australia.

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