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The influence of soil heterogeneity on exploratory tunnelling by the subterranean termite *Coptotermes frenchi* (Isoptera: Rhinotermitidae)

T.A. Evans*
CSIRO Entomology, Canberra, ACT 2601, Australia

Abstract

The exploration of sand-filled arenas by workers of an entire colony of the Australian, subterranean foraging, tree-nesting termite, *Coptotermes frenchi* Hill was investigated under laboratory conditions. The first experiment tested whether termite exploration of sand was influenced by the presence of gaps or objects in the sand. Gaps and objects were chosen to represent soil heterogeneity in the urban environment: gaps to represent tunnels dug by other animals, perspex strips to represent cables and pipes, and wood strips to represent roots. Termites always chose to explore gaps thoroughly before they began tunnelling in the sand. Significantly more and longer tunnels were excavated from the end of gaps at the far end of the arenas, and relatively little tunnelling occurred around and along objects. Termite density was significantly greater around and along wood compared with perspex blocks. The second experiment tested whether termite exploratory tunnelling was influenced by soil moisture. The termites tunnelled slowly in dry sand, but after discovering a patch of wet sand, increased tunnelling five-fold until it was completely explored, after which activity declined. Energy and water conservation may be behind these patterns of exploratory tunnelling as well as those seen in large field studies, but caution is urged when interpreting small scale laboratory experiments to explain large scale field data.

Introduction

The process by which subterranean termites (Isoptera) tunnel underground from their nesting sites to find food resources, collect food, and then return it to their nest is not well understood. That some species eat wood and find it not only in natural habitats but also in urban, built-up environments, including housing materials, is a considerable problem and is the primary fear of home owners in the warmer parts of the world (see e.g. Kofoid, 1934; Hill, 1942; Roonwal, 1979; Hadlington, 1996; Pearce, 1997) Research indicates that about one in five houses is likely to be infested by subterranean termites in Australia (Hadlington, 1996) and controlling wood-eating termites costs about $1.5 billion annually in the USA (Su & Scheffrahn, 2000). Clearly such termites are considerable pests and understanding their foraging behaviour better might help to reduce the damage that they cause.

The first step in understanding how termites forage, the documentation of the subterranean tunnel systems, began in the middle of the twentieth century, with the excavation of tunnel systems of *Coptotermes acinaciformis* (Froggatt), *C. brunneus* Gay, *C. frenchi* Hill, *C. lacteus* (Froggatt) (Rhinotermitidae) and *Nasutitermes exitiosus* (Hill) (Termitidae) in Australia (Ratcliffe & Greaves, 1940; Gay, 1946; Greaves, 1962), of *Hodotermes mossambicus* (Hagen) and *Microhodotermes viator* (Latreille) (Hodotermitidae) in South Africa (Coaton, 1958), and *C. formosanus* Shiraki, (Rhinotermitidae) in the USA (King & Spink, 1969). It was found that these termite species had large tunnel systems: between 5 and 30 tunnels from the nest, tunnels can be up to 6 cm wide and 130 m long and down to 120 cm under the soil surface. It is important to note that these termite colonies

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*Fax: +61 2 6246 4000
E-mail: theo.evans@csiro.au

and their tunnel systems were well established (the youngest colony estimate was ten years old), and these studies only considered the extent of the tunnel systems, and not how they were created or maintained.

In contrast, the way in which termites dig tunnels has been investigated only in the laboratory. These studies have used three species: *C. formosanus, Reticulitermes flavipes* (Kollar) and *R. virginicus* (Banks) (Rhinotermitidae), and have been much smaller in scale in comparison to the earlier field studies. These laboratory studies have generally used small groups of worker and soldier termites (54–1500) collected from infestations, which were allowed to tunnel in sand-filled arenas (longest linear dimension ranging from 31 to 100 cm) for one to ten days (Robson *et al.*, 1995; Chen & Henderson, 1997; Hedland & Henderson, 1999; Pitts-Singer & Forschler, 2000; Campora & Grace, 2001; Puche & Su, 2001a,b). In these tests, the termites tunnelled in all directions, but with optimal spacing (e.g. Robson *et al.*, 1995; Pitts-Singer & Forschler, 2000), tunnelled more if they had less food (Hedland & Henderson, 1999), but did not appear to detect wood even when within a few millimetres (Puche & Su, 2001a).

These laboratory studies used clean and uniform sand in their arenas. This is a stark contrast to the field studies that described very heterogeneous environments: soil composed of differing layers and mixtures of sands, clays and gravel; variable organic matter and water content; and the presence of tree roots, tunnels dug by other animals (e.g. other termite species, ants and worms). The field studies provided evidence that termites use roots and other features in the soil for making exploratory tunnelling decisions. Ratcliffe & Greaves (1940) wrote that galleries of *C. lacteus* could reach dead trees 'by following up the remains of roots'. King & Spink (1969) noted that galleries of *C. formosanus* 'followed the fissures in the clay rather than running a straight course'. There is evidence that this is true in the laboratory also. Pitts-Singer & Forschler (2000) reported that *R. flavipes* and *R. virginicus* termites almost always explored gaps in the sand in their arenas, and on average tunnelled alongside half the length of metal wires that had been pressed into the sand.

These studies have raised questions about how termites exploit soil heterogeneity in order to explore their environment. Therefore, the aim of this study was to examine the factors that influence termite forager exploration, specifically the presence of gaps and objects, and whether edible objects might be of greater interest than inedible ones. The study also aimed to quantify the influence of soil moisture in controlled laboratory conditions, as increased moisture in soil is thought to elicit termite exploration (Hadlington, 1996).

Materials and methods

A complete colony, consisting of primary reproductives, brood, workers and soldiers, of the tree-nesting termite *C. frenchi* Hill (Rhinotermitidae) was chosen because the small groups of workers and soldiers that have been used in previous laboratory experiments may not produce results representative of field situations. Laboratory studies of termites usually use groups of dozens to hundreds of foragers collected from feeding sites; these are not appropriate substitutes for colonies as isolated foragers in small groups are unlikely to behave in a similar fashion as those living in colonies. Termite colonies are extremely difficult to collect in their entirety. Fortuitously, however, this colony had established itself inside a steel drum in the field (35°17′ S, 149°13′ E, see Evans *et al.*, 1998; Evans, 2002 for details), and so was simple to retrieve. Only a single colony was used and therefore these experiments may be considered by some to be pseudoreplicated. However, colonies do not dig tunnels but rather the termites themselves do, and as there were more than 200,000 termites in this colony (several orders of magnitude larger than the number used in other studies), it would seem unlikely that the same termites dug all replicates.

The steel drum containing the colony (27 cm × 23 cm diameter) was installed in a climate-controlled laboratory (26°C and 70% rh) in January 2001, with wood of *Eucalyptus regnans* F. Muell. (Myrtaceae) and water. Forager movement and tunnelling behaviour were observed in three perspex arenas positioned at a distance of about 100 cm around the drum containing the nest. The arenas were made from two sheets of perspex (120 cm × 120 cm) held apart by strips of steel (119 cm × 1 cm × 0.2 cm) that were screwed into place around the edges of the bottom perspex sheet, and were connected to the nest drum using a plastic tube (fig. 1). The width of the arena was constrained by the width of the perspex sheet produced by the manufacturer, and the depth (0.2 cm) was determined by termite size, i.e. it was shallow enough to ensure that all tunnels and termites were visible. The arenas were filled with clean, dry, sifted sand (particle size < 500 μm) into which the experimental materials were positioned (see below). The arenas were horizontal and level with the base of the nest drum, so as to simulate more field-like conditions in the laboratory.

Objects and gaps

Three types of soil heterogeneity that might influence termite tunnelling were tested in this experiment: edible objects, non-edible objects and gaps. The first were intended to simulate roots, represented here by wood strips of *E. regnans*, the second were intended to simulate stones, foundations, pipes or cables, represented here by perspex strips, and the third were based on tunnels dug by other animals, represented here by gaps created by removing sand. These were tested separately and in combination in five treatments called: wood, perspex, gap, wood + gap and perspex + gap. The consistency of any influence of these treatments was assessed by offering them twice, in succession, called first and second choices.

The sand in the arenas was moistened uniformly. A thin section of sand was removed along the entire edge of the arena near to the nest drum to create an initial, front gap (0.5 cm wide). The tube that connected the nest drum to the arena led to this front gap so that the termites would have free movement along the entire edge with no tunnelling effort required. The 'first choice' treatments were placed at 20 cm intervals along and perpendicular to the front gap (as shown in fig. 2a). The objects were the same size (35 cm × 1 cm × 0.2 cm) whereas the gaps were half the width (35 cm × 0.5 cm × 0.2 cm).

At the far end of each of the first choice treatments, three 'second choice' treatments were placed along a 10 cm 'boundary' gap (see fig. 2a). The three second choices were always object, gap, and object + gap, with the positions assigned randomly along the 10 cm boundary. Wood was

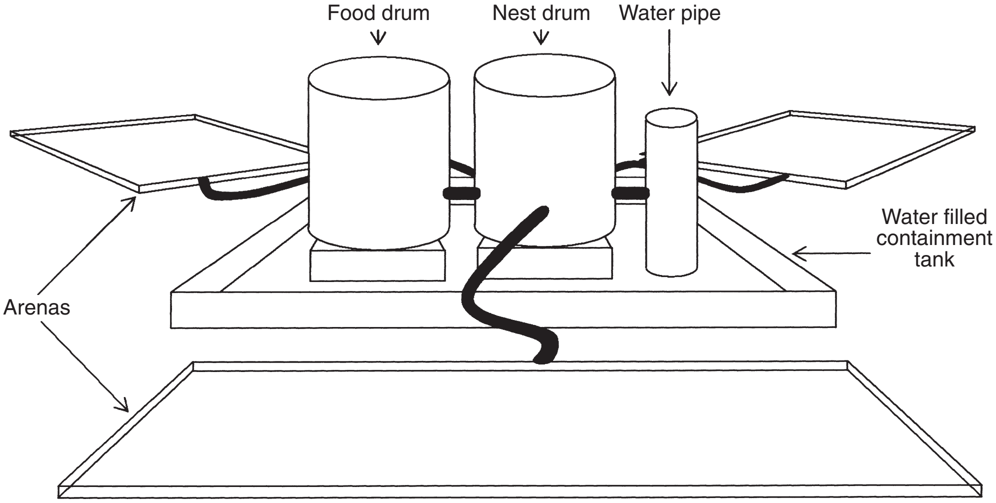


Fig. 1. The set up of the apparatus. The steel drums containing the *Coptotermes frenchi* nest and food (both 27 cm × 23 cm diameter) were placed on bricks in a water-filled tank for containment of the termites. Termites could obtain water from the sand-filled PVC pipe (30 cm × 9 cm diameter) that sat in the water of the containment tank. Three perspex arenas (120 × 120 × 0.5 cm) were placed around the containment tank. The drums, water pipe and arenas were all connected with plastic tubing (1 cm diameter, coloured black). N.B. the benches on which the apparatus was assembled are not shown.

used as the object for the wood, gap and wood + gap first choices, and perspex was used as the object for the perspex and perspex + gap first choices. The second choices were the same size as the first choices (fig. 2a). No first choice was aligned with the connecting tube, and no second choice was aligned with the first choice, so that the termites could not simply continue moving forwards without making a decision.

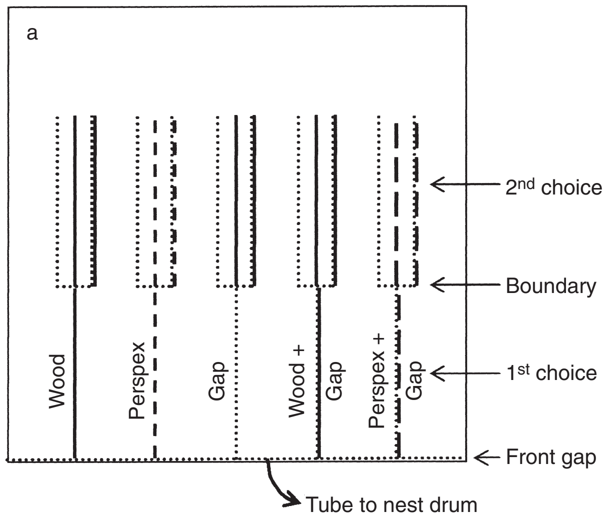
After the treatments were positioned, the top sheet of perspex was placed carefully over the top and secured with large binder clips. Bowing of the top perspex sheet was prevented by placing 15 transparent perspex boxes (25 × 19 × 10 cm) half-filled with water on the arena, which placed *c.* 40 kg of pressure reasonably uniformly over the entire surface. A sheet of cardboard (1.2 × 1.2 m) and a black plastic sheet (1.8 × 1.8 m) covered the arenas in order to provide darkness and encourage termite exploration. Each arena was used twice, producing six replicates. The arenas were cleaned thoroughly between experiments and new sand and solid objects were used for each replicate.

Observations were made at 24 h intervals over four days by lifting the black plastic sheet and cardboard and peering through the perspex boxes and water. The maximum distance along each choice explored by the termites was measured, and the density of termites along each choice was determined. All tunnels, their position of origin and length were recorded. The number of tunnels was determined as the number of points where termites were excavating. For example, using this rule, a single tunnel that divided into two (creating a 'Y' pattern) would be counted as two tunnels. The length of all the tunnels on each day was added for analysis, because using the above rule, it was difficult to ascertain the original from secondary tunnels. The arenas were typically explored to their edges after four days, with all solid objects and gaps interconnected with many tunnels. Consequently, comparisons were made at days 1, 2 and 3.

Water

The sand used in this experiment was dried in an oven (80°C for 4 h, until weight did not change) and allowed to cool before being placed into the arenas. A perspex slat (40 cm × 4 cm) was placed carefully on top of the sand 100 cm from the front of the arena, touching either the left or right side. Water (100 ml) was poured slowly on top of this slat, which allowed a more even distribution of water over the sand with a minimum of sand disturbance. This created a patch of wet sand with a wetter centre and drier periphery, of about 70 cm × 30 cm (see fig. 2b). The slat was removed, the sand was levelled carefully and the arena was covered with the top sheet of perspex and secured with the binder clips as before. A sheet of clear plastic was placed on the arena, which was then covered with the water-filled boxes, cardboard and black plastic as before.

Observations were made as before, and all tunnelling was traced onto the clear plastic sheet. The experiment ran until the arena had been explored completely, which took up to 20 days. Three phases were designated according to tunnelling activity. 'Phase 1' was when the termites were tunnelling only in the dry sand before the patch of wet sand was encountered. The time taken for the termites to encounter the wet sand was noted, and the number of tunnels and the total length of tunnels excavated in the dry sand on each day during phase 1 was calculated (as above). 'Phase 2' was the exploration of the patch of wet sand. The time taken for the termites to explore the patch of wet sand completely was noted, and the number of tunnels and the total length of tunnels excavated in the wet sand and in the dry sand on each day during this phase were calculated. 'Phase 3' was designated as the period after the patch of wet sand was explored. This was continued for a few days only; depending on how long the experiment had been running and whether the termites had damaged the plastic tubes



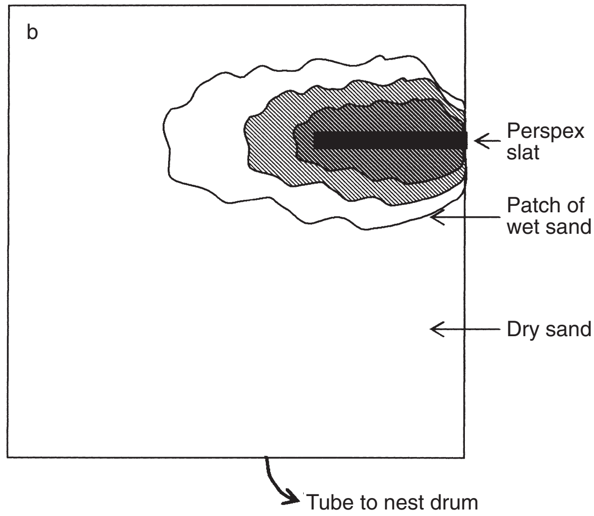


Fig. 2. A schematic plan view of the arenas (120 × 120 × 0.5 cm) used in the laboratory experiments. (a) The arena used for the 'objects and gaps' experiment, the first and second choice treatments were 35 × 1 × 0.2 cm. Symbols: solid line, wood; dashed line, perspex; dotted line, gap. (b) The arena used for the 'water' experiment. The black strip represents the perspex slat used in the application of the water; the irregular lines represent the spread of water to form the patch of wet sand.

connecting the arena to the nest drum. Two sequential runs were performed in all three arenas, producing six replicates. The arenas and perspex solid objects were cleaned thoroughly between experiments and new sand was used for each run.

Analyses

In the object and gap experiment, the distance explored, the density of termites, the number and length of tunnels originating from both the sides and the far end of the first choices were compared between first choice treatments using repeated measures ANOVA, as each of these variables was measured repeatedly over the three days. Second choices with wood were always separated from second choices with perspex; therefore these results were analysed using presence of a gap: gap, wood + gap and perspex + gap were combined to become 'with gap', whereas wood and perspex were combined to become 'no gap'. Then distance explored, termite density, side and far end tunnel number and length for second choices were compared using repeated measures ANOVA with two factors (first choice and second choice). Termite density was also compared using unpaired *t*-tests between second choices with and without wood (i.e. wood + gap vs. perspex + gap, and wood vs. perspex), but only on day 3 once tunnel construction was at its greatest. The data met parametric requirements and so were not transformed.

In the water experiment, the number and length of tunnels dug simultaneously in the wet sand and in the dry sand were compared for five days in phase 2 and for three days in phase 3 using repeated measures ANOVA. The rate of tunnelling in dry sand was compared between phases 1, 2 and 3 using one way ANOVA on log transformed data to meet homoscedasticity requirements (Sokal & Rohlf, 1995). Interaction terms were not noted unless they were significant, and all post hoc comparisons for all analyses were Bonferroni-corrected. Systat 9 (SPSS Inc., Chicago) was used for all statistical analyses.

Results

Objects and gaps

Exploration of initial front gap

Workers of *C. frenchi* entered the arenas quickly after the nest-drum was connected to the arena, only 3 h had elapsed and termites were seen along the entire length of the front gap. This suggested that the distance of the first choices from the entrance of the connecting tube would not be a major influence on where the termites might choose to explore. Very few tunnels were dug along the front gap. Almost all tunnels that originated from the front gap were excavated at the two ends, along the side edges of the arena. Thus there was a mean of 1.67 ± 0.42 (SE) tunnels excavated by the end of day 1, with a slight increase to 2.50 ± 0.43 tunnels by day 2, but no change by day 3 (2.50 ± 0.34 tunnels). The mean length increased daily, from 11.0 ± 3.41 cm on day 1 to 22.3 ± 7.09 cm on day 2 to 29.8 ± 10.2 cm by day 3.

Distance explored along first choices

All first choices with a gap in the sand were explored quickly and completely, whereas those without a gap were almost ignored. All but one replicate of 'gap' and all wood + gap and perspex + gap were fully explored (35 cm) on day 1, compared with a mere 5 cm of wood and 0 cm of perspex being explored by day 3 (fig. 3a). The distance travelled along the first choices was significantly different between treatments ($F_{4,25} = 387.9$, $P < 0.001$). This was entirely due to the presence of a gap, as gap, wood + gap and perspex + gap were not significantly different (Bonferroni-corrected post hoc comparisons $P > 0.05$), neither were wood and perspex ($P > 0.05$) but all comparisons between these groups of treatments were ($P < 0.05$). The distance explored by the

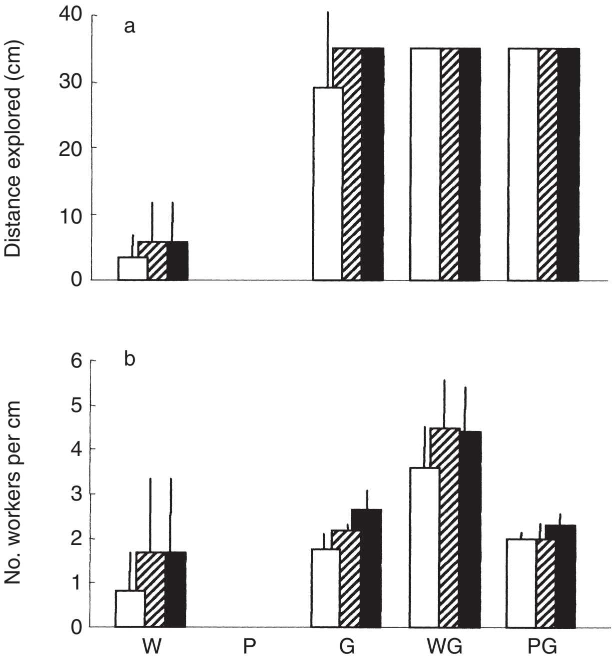


Fig. 3. (a) The average distance (± SE) travelled by *Coptotermes frenchi* along the first choice treatments, and (b) the average density (± SE) of termites observed in the 'objects and gaps' laboratory experiment. Symbols: W, wood; P, perspex; G, gap; WG, wood + gap; PG, perspex + gap; □, day 1; ▨, day 2; ■, day 3.

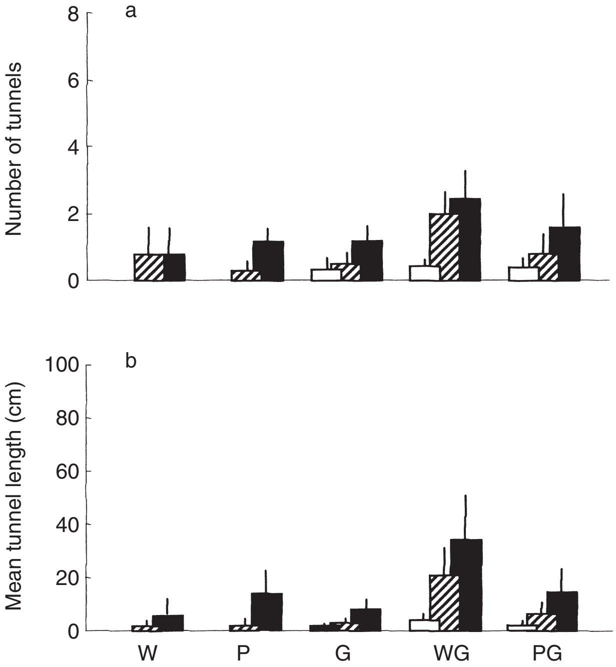


Fig. 4. (a) The average number of tunnels (± SE) originating at the far end of the first choice treatments (i.e. the boundary gap), and (b) the average total length of the tunnels (± SE) dug by *Coptotermes frenchi* in the 'objects and gaps' laboratory experiment. Symbols as in fig. 3.

termites did not change significantly over the 3 days as the repeated factor was not significant ($F_{2,50}$ = 1.537, P = 0.225).

Termite density along first choices

There were significantly different densities of termites in the first choice treatments ($F_{4,25}$ = 15.37, $P < 0.001$), with those sections of sand with wood + gap having about double the number of termites compared with gap and perspex + gap or wood, and all with more than perspex ($P > 0.05$) (fig. 3b). The numbers of termites tended to increase over the three days, but this was not significant (repeated factor $F_{2,50}$ = 3.131, P = 0.052).

Tunnel excavation from first choices

There was little tunnel excavation extending laterally from the sides of the first choices, and almost all of this occurred in two replicates of wood + gap. By day 3, the termites had excavated no tunnels at all from the sides of the wood, perspex and perspex + gap treatments, only 0.5 ± 0.3 tunnels of total length 3.3 ± 2.1 cm from the sides of the gap treatment, but 2.9 ± 2.0 tunnels of total length of 30.9 ± 23.5 cm from the sides of the wood + gap treatment. The large standard errors are indicative of the large variation between replicates, consequently, these differences were not significant either for number of tunnels ($F_{4,25}$ = 1.333, P = 0.285), or for tunnel length ($F_{4,25}$ = 1.276, P = 0.306). Time was not significant either (tunnel number: repeated factor $F_{2,50}$ = 1.069, P = 0.351; tunnel length: repeated factor $F_{2,50}$ = 1.379, p = 0.261).

There was greater tunnel excavation at the far ends than laterally from the sides of the first choice treatments. There were no significant differences between first choices either in the number of tunnels ($F_{4,25}$ = 1.367, P = 0.274), or in tunnel length ($F_{4,25}$ = 1.703, P = 0.181),but there were significant differences between days as the termites excavated more (repeated factor $F_{2,50}$ = 11.93, $P < 0.001$) and longer tunnels over time (repeated factor $F_{2,50}$ = 7.55, P = 0.001) (fig. 4).

Distance explored along second choices

As observed for the first choice treatments, termites explored the second choice treatments with gaps in the sand quickly (fig. 5a). The fastest exploration occurred when the first choice treatment included a gap also: the termites traversed the first and the second choice treatment gaps on the first day. Slower exploration of second choice treatments 'with gap' occurred when the first choice treatment did not have a gap (i.e. perspex and wood). These second choice treatments were reached by day 3, after the termites had tunnelled from the boundary gaps of first choice treatments with gaps. There was little exploration along second choices that were categorized as 'no gap', regardless of whether they had a first choice with a gap or without (table 1). This pattern was evident from the analysis: the presence of a gap in the sand was significant for first choice ($F_{1,86}$ = 53.7, $P <$ 0.001), second choice ($F_{1,86}$ = 177.0, $P < 0.001$), and the interaction was significant also ($F_{1,86}$ = 54.2, $P < 0.001$). The repeated measure factor was also significant (F_{2172} = 29.7, P < 0.001), as were the interactions between first choice and repeated measure (F_{2172} = 6.52, P = 0.002) and second choice and repeated measure (F_{2172} = 4.20, P = 0.017). This indicated

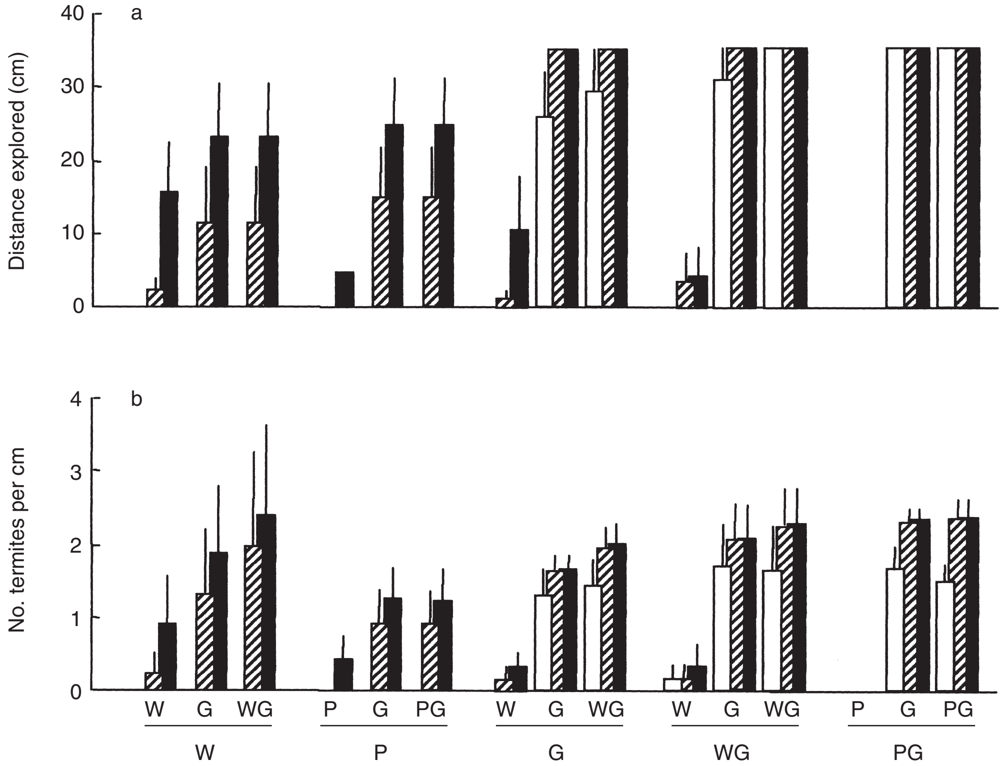


Fig. 5. (a) The average distance (± SE) travelled by *Coptotermes frenchi* along the second choice treatments, and (b) the average density (± SE) of termites observed in the 'objects and gaps' laboratory experiment. Symbols as in fig. 3.

Table 1. The mean distance explored and mean density (± SE) of *Coptotermes frenchi* along second choice treatments over the three days of the objects and gaps experiment.

First choice	Second choice	N	Distance travelled (cm)			Termite density (no./cm)		
			Day 1	Day 2	Day 3	Day 1	Day 2	Day 3
With gap	With gap	36	29.7 ± 2.0^{a}	35.0 ± 0.0^{b}	35.0 ± 0.0^{b}	1.5 ± 0.2^{a}	2.4 ± 0.2^{b}	2.4 ± 0.2^{b}
With gap	No gap	18	0.6 ± 0.6^{c}	1.9 ± 1.3^{c}	6.7 ± 3.0^{d}	0.1 ± 0.1^{c}	0.2 ± 0.1^{c}	0.4 ± 0.2^{c}
No gap	With gap	24	0.0 ± 0.0^{c}	11.7 ± 3.4^{d}	23.3 ± 3.4^{e}	0.0 ± 0.0^{c}	0.8 ± 0.3^{d}	1.3 ± 0.2^{e}
No gap	No gap	12	0.0 ± 0.0^{c}	0.8 ± 0.8^{c}	8.0 ± 4.1^{d}	0.0 ± 0.0^{c}	0.1 ± 0.1^{c}	0.4 ± 0.2^{c}

'With gap' refers to either gap, wood + gap or perspex + gap, and 'no gap' refers to either wood or perspex. Significant differences are indicated by superscript letters: comparisons down columns are differences between factors (i.e. with gap vs. no gap) and comparisons along rows are differences over time (the repeated measure). N.B. Separate analyses conducted for distance and density.

that the distance travelled along the second choices increased over the three days, but did so at differing rates.

Termite density along second choices

The densities of termites along the second choice treatments corresponded generally with the distances explored: more termites were recorded along second choices 'with gap' that were connected to first choices 'with gap' than other combinations, and the least number of termites were found in the 'no gap' plus 'no gap' choice combinations (table 1, fig. 5b). Gap presence was significant for first choice ($F_{1,86} = 14.8$, $P < 0.001$) and second choice ($F_{1,86} = 42.3$, $P < 0.001$), and the interaction between first and second choice factors was significant ($F_{1,86} = 12.6$, $P < 0.001$), as found for distance explored (above). The repeated measure factor was also significant ($F_{2172} = 18.9$, $P < 0.001$), showing that termite density increased with time. However, the interaction between time (the repeated measure) and first choice was not significant ($F_{2172} = 0.37$, $P = 0.693$), whereas that with second choice was ($F_{2172} = 5.73$, $P = 0.004$), which showed that termite density had increased by day 3 in those second choices 'with gaps' that had been blocked by 'no gap' first choices. Termites densities were higher but not significantly so when wood was present. This was true for the treatments 'with gaps' (wood + gap 2.25 ± 0.32 cf. perspex + gap 1.80 ± 0.17 termites cm^{-1}; $t_{58} = 1.14$, $P = 0.257$), and those that had 'no gap' (wood 0.53 ± 0.24 cf. perspex 0.25 ± 0.23 termites cm^{-2}; $t_{28} = 0.814$, $P = 0.423$).

Tunnel excavation along second choices

There were very few tunnels excavated by the termites along the sides of the second choices and these were very short. By day 3, the majority of the few tunnels that were dug along the sides of the second choices were found in the 'with gap' second choice treatments connected to 'with gap' first choices (0.3 ± 0.1 tunnels, 3.3 ± 1.4 cm long). There was almost no tunnelling along the 'with gap' plus 'no gap' treatment combinations (0.1 ± 0.1 tunnels, 0.6 ± 0.5 cm long), and there was no tunnelling at all in the 'no gap' plus 'no gap' choice combinations. These small differences were not significant for first choice treatment ($F_{1,86} = 1.91$, $P = 0.170$), for second choice treatment ($F_{1,86} = 2.15$, $P = 0.146$), or for the repeated measure factor ($F_{1,86} = 3.22$, $P = 0.076$).

In stark contrast, the termites excavated more frequently and produced longer tunnels at the far end of the second choices. The differences in far end tunnel construction between the second choices corresponded generally with the distances explored and termite density: more and longer tunnels were excavated from second choice treatments 'with gap' connected to first choice treatments 'with gap' than other treatment combinations (table 2, fig 6). The same pattern of significant differences was found for tunnel excavation as for the other parameters. Termites excavated significantly more ($F_{1,86} = 12.4$, $P = 0.001$) and longer tunnels ($F_{1,86} = 10.9$, $P = 0.001$) in 'with gap' first choices and significantly more tunnels ($F_{1,86} = 29.8$, $P < 0.001$) and longer tunnels ($F_{1,86} = 20.8$, $P > 0.001$) in 'with gap' second choices. The interaction between first and second choice treatments

Table 2. The mean number and total length (± SE) of tunnels excavated by *Coptotermes frenchi* at the far end of second choice treatments over the three days of the experiment.

First choice	Second choice	N	Number of tunnels			Tunnel length (cm)		
			Day 1	Day 2	Day 3	Day 1	Day 2	Day 3
With gap	With gap	36	1.6 ± 0.2^{a}	2.8 ± 0.4^{b}	3.5 ± 0.5^{b}	6.8 ± 1.3^{a}	21.8 ± 3.3^{b}	40.2 ± 5.9^{c}
With gap	No gap	18	0.0 ± 0.0^{c}	0.0 ± 0.0^{c}	0.1 ± 0.1^{c}	0.0 ± 0.0^{c}	0.0 ± 0.0^{c}	0.2 ± 0.2^{c}
No gap	With gap	24	0.0 ± 0.0^{c}	0.5 ± 0.2^{d}	1.2 ± 0.2^{e}	0.0 ± 0.0^{c}	2.5 ± 1.0^{d}	8.5 ± 1.8^{e}
No gap	No gap	12	0.0 ± 0.0^{c}	0.0 ± 0.0^{c}	0.2 ± 0.2^{c}	0.0 ± 0.0^{c}	0.0 ± 0.0^{c}	1.2 ± 0.8^{c}

'With gap' refers to either gap, wood + gap or perspex + gap, and 'no gap' refers to either wood or perspex. Significant differences are indicated by superscript letters: comparing down columns are differences between factors (i.e. with gap vs. no gap) and comparisons along rows are differences over time (the repeated measure). N.B. Separate analyses conducted for number and length of tunnels.

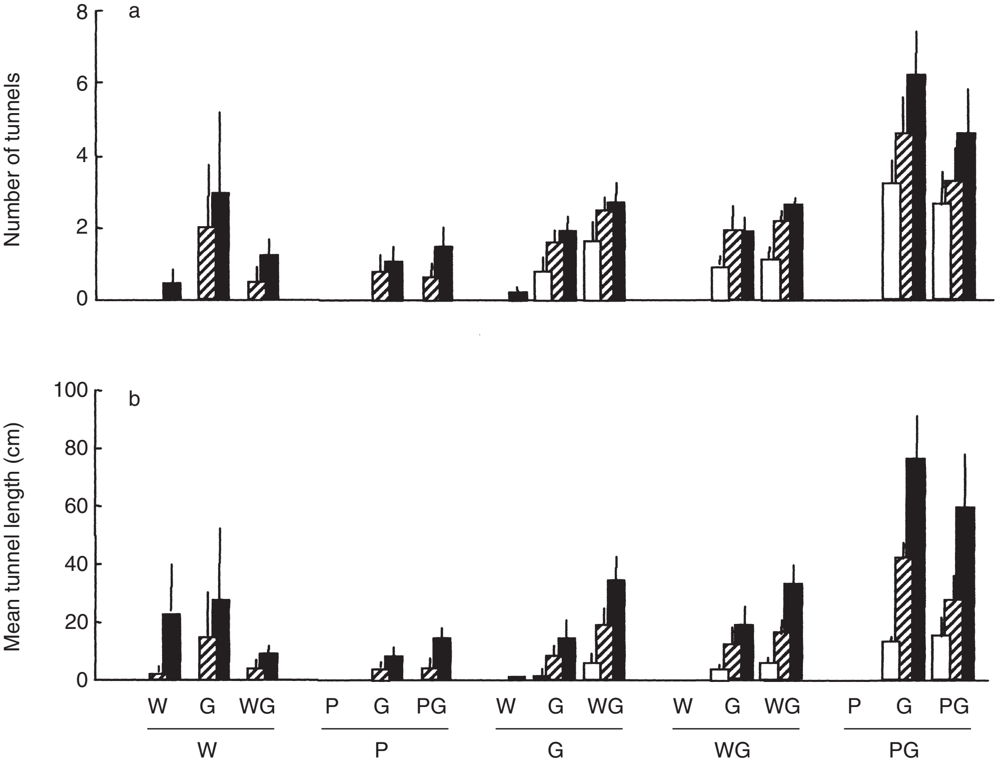


Fig. 6. (a) The average number of tunnels (± SE) originating at the far end of the second choices, and (b) the average total length of the tunnels dug by *Coptotermes frenchi* in the 'objects and gaps' laboratory experiment. Symbols as in fig. 3.

was significant, for both the number of tunnels ($F_{1,86} = 14.0$, $P < 0.001$) and their length ($F_{1,86} = 11.6$, $P = 0.001$). The repeated measure factor was significant, showing that termites excavated significantly more tunnels ($F_{2172} = 13.7$, $P < 0.001$) and longer ($F_{2172} = 18.8$, $P > 0.001$) tunnels over time.

Water

The time taken for the termites to encounter the wet sand, and therefore the duration of phase 1, varied from five to 16 days (mean ± SE, 10.8 ± 1.8 days). The termites were digging approximately three tunnels in the dry sand on any day during phase 1 and the total length of these tunnels was less than 20 cm per day (table 3, fig. 7).

Phase 2, the period when the termites were exploring the patch of wet sand, lasted from two to eight days (mean ± SE, 4.2 ± 0.9 days). The termites dug about four times the number of tunnels in the wet sand compared with the dry sand on any one day during this period; this difference was significant ($t_{26} = 3.84$, $P = 0.001$). The tunnels that the termites dug in the wet sand were about five times longer compared with those in the dry sand, which was a significant difference ($t_{26} = 526$, $P < 0.001$) (table 3, fig. 7).

During phase 3 there was a steep decline in termites tunnelling in the wet sand and an increase in their tunnelling in dry sand. The termites dug around four times as many tunnels that were approximately four times as long in the dry sand compared with the wet sand on any day during this period (table 3, fig. 7). Both differences were

Table 3. The mean number and total length of tunnels (± SE) dug by *Coptotermes frenchi* during the three phases of the water experiment.

Tunnel	Phase 1	Phase 2		Phase 3	
	Dry sand	Dry sand	Wet sand	Dry sand	Wet sand
Number	2.9 ± 0.4 ^{a}	5.7 ± 1.5 ^{b}	26.0 ± 5.9 ^{c}	23.0 ± 4.2 ^{c}	5.8 ± 1.5 ^{b}
Length	17.2 ± 1.6 ^{a}	23.1 ± 4.0 ^{a}	138.3 ± 37.4 ^{b}	120.6 ± 31.5 ^{b}	23.1 ± 6.0 ^{a}

Significant differences are indicated by superscript letters. N.B. Separate analyses conducted for number and length of tunnels.

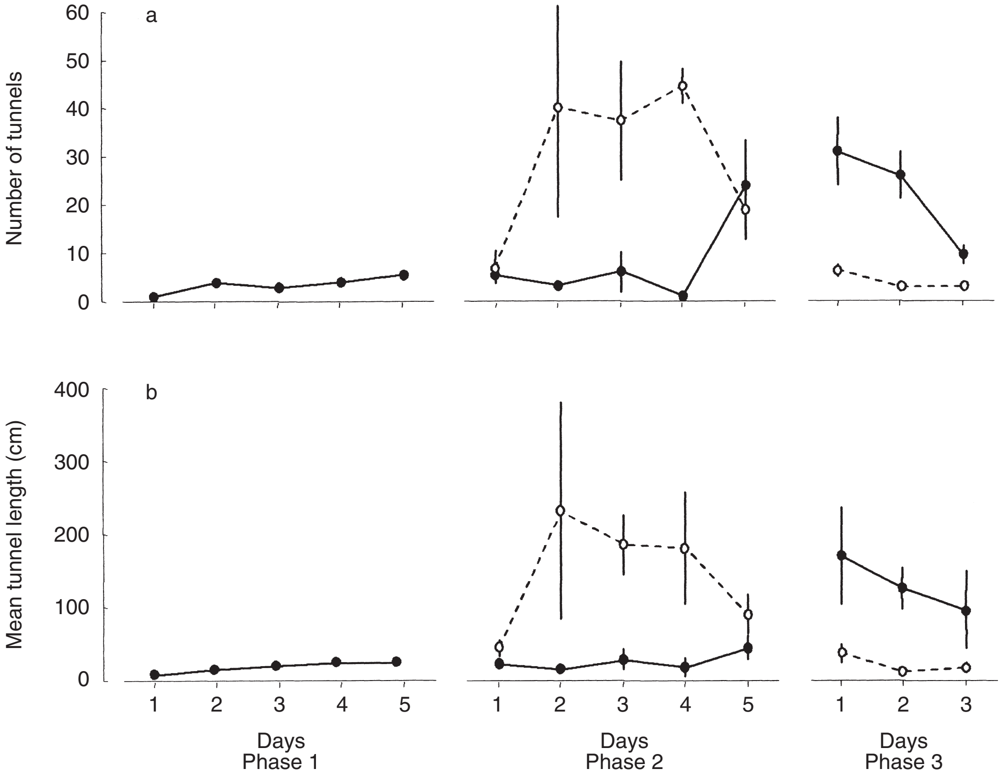


Fig. 7. The average number and total length of tunnels (± SE) in dry sand (-●-) and wet sand (--○--) dug by *Coptotermes frenchi* during the three phases of the water experiment. Phase 1, before the wet sand had been discovered; phase 2, during exploration of the wet sand; phase 3, after complete excavation of the wet sand. Although the phases are sequential, they were of different duration in each replicate. Therefore the number of days depicted for each phase was reduced to the lowest amount, and the lines are shown as discontinuous.

significant (number of tunnels, $t_7 = 4.92$, $P = 0.002$, total tunnel length, $t_7 = 3.56$, $P = 0.009$).

Although the termites doubled the number of tunnels being dug in the dry sand from phases 1 to 2, a significant increase ($t_{23} = 2.37$, $P = 0.026$), the total length of these tunnels was not significantly different ($t_{21} = 1.11$, $P = 0.278$). There was a significant four fold increase in termite tunnelling in the dry sand from phases 2 to 3, with the construction of more ($t_7 = 11.38$, $P < 0.001$) and longer tunnels ($t_7 = 4.24$, $P = 0.004$) (table 3, fig. 7). .

Discussion

Workers of *C. frenchi* explored gaps in the sand relatively quickly, with the entire distance of the front gap, first choice treatments with gaps and second choice treatments with gaps explored by the end of day 1 in almost all replicates (a total distance of *c.* 465 cm). In comparison, the *C. frenchi* workers were least interested in exploring along objects in the sand that did not have a gap, although wood alone attracted greater interest (*c.* 10 cm by day 3) than perspex alone (*c.* 5 cm by day 3) (see figs 2 and 5).

This should not be a surprising result as the workers of *C. frenchi* simply explored the least energetically demanding route. As mentioned in the introduction, King & Spink (1969) noted that *C. formosanus* galleries 'followed the fissures in the clay.' Pitts-Singer & Forschler (2000) considered that the *Reticulitermes* spp. termites in their laboratory experiment were minimizing energetic costs by following the gaps in the sand: this occurred in almost all replicates whereas tunnelling alongside the complete length of buried objects occurred in only half. The *Reticulitermes* termites did tunnel alongside inedible objects, whereas *C. frenchi* termites in this experiment did not (see fig. 3). Perhaps this is due to species differences, or possibly due to the larger apparatus used in this study (Pitts-Singer & Forschler, 2000).

The tunnels excavated by *C. frenchi* workers were concentrated almost entirely at the far ends of the gaps. There were three of these: at the ends of the front gaps (on the left and right sides of the arena), at the far end of the first choices (off the boundary gaps), and at the far end of the second choices. After three days, these tunnels were up to four times more numerous and up to nine times longer compared with tunnels excavated elsewhere. The pattern suggested that the termites were travelling as far as they could from the nest with the least effort by following the existing gaps, before they expended any energy digging tunnels.

Eucalyptus wood was used in this experiment to determine whether a potentially edible object was of greater interest than an inedible one. There were few significant differences found between objects made of wood and perspex (e.g. further tunnelling and greater termite density along first choices), thus the role of edible solid objects appeared to be small. This does not appear to be true from field studies: several species have been shown to tunnel within and under roots, such as *C. acinaciformis*, *C. brunneus*, *C. formosanus*, *C. frenchi* and *C. lacteus* (Ratcliffe & Greaves, 1940; Gay, 1946; Greaves, 1962; King & Spink, 1969), although species differences may exist as *N. exitiosus* '… showed a much greater tendency to follow roots then did the galleries of *C. lacteus*' (Ratcliffe & Greaves, 1940). These termites may simply use roots to find their primary food sources – living and dead trees. Greaves (1962) noted succinctly that '… the galleries followed old roots for most of the way to an old eaten-out stump' (p. 644); he also observed that *C. acinaciformis* and *C. brunneus* entered trees via their roots in about 50% of cases. *Neotermes* in plantations in Fiji also follow roots (by eating them from the inside) to travel between trees (M. Lenz & R. Eldridge, personal communication).

Timber sitting on the soil surface does not have the same effect; termites do not tunnel along such food sources. Ratcliffe & Greaves (1940) noted that for *C. lacteus*: 'the connexion between a gallery and a food mass generally took the form of a steeply-rising branch coming off at a point either directly under or very close to the log. The gallery itself, when travelling further, would maintain its depth, and without faltering in its course pass under the log up to which the 'feeding branch' or branches had risen' (p. 155). This was also observed by Greaves (1962) for *C. acinaciformis* and *C. brunneus*, and fig. 1 of King & Spink (1969) suggests this for *C. formosanus*. This pattern suggests that termites are capable of detecting surface wood once they pass underneath it, perhaps by breakdown products that leach into the soil (e.g. Esenther *et al.*, 1961) or by temperature or moisture shadows (e.g. Ettershank *et al.*, 1980).

Puche & Su (2001a) observed that *C. formosanus* termites did not detect wood in their laboratory tests. Perhaps the lack of response by *C. formosanus* observed by Puche & Su (2001a) and a similar disinterest by *C. frenchi* found in the present study was due to two aspects of the laboratory setup. First, the size of the wood block used was small: 6.5 cm diameter × 0.3 cm (Puche & Su, 2001a) and 35 × 1 × 0.2 cm (present study), especially so for termites that have evolved to eat trees. The size of a food resource affects foraging behaviour; termites consume small resources slowly, perhaps to conserve them (Lenz, 1994); and they tunnel further, perhaps to find new resources faster (Hedland & Henderson, 1999). Second, the surface wood in the field studies had time to weather and so perhaps alter the soil underneath, thus creating the signals required by the termites to find it – time that was absent from laboratory studies.

This should warn of the difficulties in comparing laboratory tests with field observations, especially for tunnel systems in termites. The large and complex tunnel systems excavated by termite colonies are formed over many years and are constructed as colonies grow. Some parts of tunnel systems may be maintained for many years, but other parts will become obsolete as the food resources they service are consumed; e.g. a 'disused and blocked gallery was discovered… and it was possible to trace it for some feet by the discolouration of the soil' (Ratcliffe & Greaves, 1940 p. 158). Of course new food sources will be discovered and the laboratory studies of tunnelling behaviour may yield valuable insights into this process. However, interpreting data from very small scale laboratory experiments to explain large scale phenomena is fraught, and caution is noted by several authors (Hedland & Henderson, 1999; Pitts-Singer & Forschler, 2000).

Water was a very important influence in *C. frenchi* tunnelling behaviour, at least in the homogeneous sand of the water experiment. Termites tunnelled slowly in the dry sand, but diverted their tunnelling into the wet sand once it had been discovered. The termites increased their rate of tunnelling five-fold once they encountered the extremities of the patch of wet sand, and furthermore they headed directly into the centre of the wet patch. In just four days the wet patches had been completely explored, after which the termites decreased their tunnelling therein, showing that the termites recognized where they had been; and then increased their tunnelling activity in the dry sand (fig. 7).

This finding was not a novel insight; water has long been known to be of great importance for termites. Ratcliffe & Greaves (1940) noted in their field study of *C. lacteus* that tunnels descended for water 'at various points along the galleries, but particularly in the neighbourhood of food masses.' Greaves (1962) reported that the arid zone-living *C. brunneus* had galleries (tunnels) with walls up to 18 mm thick, possibly to reduce water loss, and that the vertically descending 'shafts' were more common than seen for *C. acinaciformis*, *C. lacteus* or *N. exitiosus* that live in wetter areas of Australia (Ratcliffe & Greaves, 1940; Greaves, 1962). King & Spink (1969) also found thick, cartonous lining around tunnels and vertical 'shafts' excavated by *C. formosanus* in Louisiana, which they reported were more common than observed for *C. acinaciformis*, *C. brunneus* and *C. lacteus*.

Subterranean termites inhabit a very heterogeneous world, and the results of this laboratory study suggest that *C. frenchi* uses heterogeneity to its advantage. This species followed gaps in the sand quickly to the most distant points and started to tunnel at the extremities, thus maximizing the area explored and creating a diffuse tunnel network. That gaps and objects were used even on the small scale of this laboratory experiment, may be of consequence and requires further investigation for future studies of termite exploratory tunnelling behaviour, especially in the field with whole termite colonies. Many observers have noted how termites appear to use pipes leading to houses, such as water and sewer pipes, and conduit pipes containing electrical cables. Gaps in the soil usually form underneath pipes and roots, due to the flow of water in the soil, and this appears to be true in urban areas, perhaps due to the movement of sand and soil during construction. There are several commercial products that attempt to restrict the passage of termites along pipes at the point of entry of the pipe into the house (e.g. Tamashiro *et al.*, 1991; Lenz & Runko, 1994). This may prove to be a valuable approach, if the results of this study are indicative.

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References

Campora, C.E. & Grace, J.K. (2001) Tunnel orientation and search pattern sequence of the Formosan subterranean termite (Isoptera: Rhinotermitidae). *Journal of Economic Entomology* **94**, 1193–1199.

Chen, J. & Henderson, G. (1997) Tunnel and shelter tube convergence of Formosan subterranean termites (Isoptera: Rhinotermitidae) in the laboratory. *Sociobiology* **30**, 305–318.

Coaton, W.G.H. (1958) The hodotermitid harvester termites of South Africa. Science Bulletin No. 375, Department of Agriculture (South Africa) 112 pp.

Esenther, G.R., Allen, T.C., Casida, J.E. & Shenefelt, R.D. (1961) Termite attractant from fungus infected wood. *Science* **134** (3471), 50.

Ettershansk, G., Ettershansk, J.A. & Whitford, W.G. (1980) Location of food resources by subterranean termites. *Environmental Entomology* **9**, 645–648.

Evans, T.A. (2002) Tunnel specificity and forager movement in subterranean termites (Isoptera: Rhinotermitidae and Termitidae). *Bulletin of Entomological Research* **92**, 193–201.

Evans, T.A., Lenz, M. & Gleeson, P.V. (1998) Testing assumptions of mark-recapture protocols for estimating population size using Australian, mound-building, subterranean termites. *Ecological Entomology* **23**, 101–121.

Gay, F.J. (1946) A case of house infestation by a tree-dwelling colony of *Coptotermes frenchi* Hill. *Journal of the Council of Scientific and Industrial Research* **19**, 330–334.

Greaves, T. (1962) Studies of foraging galleries and the invasion of living trees by *Coptotermes acinaciformis* and *C. brunneus* (Isoptera). *Australian Journal of Zoology* **10**, 630–651.

Hadlington, P.W. (1996) *Australian termites and other common timber pests*. Sydney, University of New South Wales Press.

Hedland, J.C. & Henderson, G. (1999) Effect of food size on search tunnel formation by the Formosan subterranean termite (Isoptera: Rhinotermitidae). *Journal of Economic Entomology* **92**, 610–616.

Hill, G.F. (1942) *Termites (Isoptera) of the Australian region*. Melbourne, Australia, Council of Scientific and Industrial Research.

Kofoid, C.A. (1934) *Termites and termite control*. Berkeley, California, University of California Press.

King, E.G. & Spink, W.T. (1969) Foraging galleries of the Formosan subterranean termite *Coptotermes formosanus* in Louisiana. *Annals of the Entomological Society of America* **62**, 536–542.

Lenz, M. (1994) Food resources, colony growth and caste development in wood-feeding termites. pp. 159–209 *in* Hunt, J.H. & Nalepa, C.A. (*Eds*) *Nourishment and evolution in insect societies*. Boulder, Colorado, Westview Press.

Lenz, M. & Runko, S. (1994) Protection of buildings, other structures and material ground contact from attack by subterranean termites (Isoptera) with a physical barrier – a fine mesh of high grade stainless steel. *Sociobiology* **24**, 1–16.

Pearce M.J. (1997) *Termites: biology and pest management*. New York, CAB International.

Pitts-Singer, T.L. & Forschler, B.T. (2000) Influence of solid object lines and passageways on tunnelling behaviour of *Reticulitermes flavipes* (Kollar) and *R. virginicus* (Banks) (Isoptera: Rhinotermitidae). *Journal of Insect Behaviour* **13**, 273–290.

Puche, H. & Su, N.-Y. (2001a) Tunnel formation by *Reticulitermes flavipes* and *Coptotermes formosanus* (Isoptera: Rhinotermitidae) in response to wood in sand. *Journal of Economic Entomology* **94**, 1398–1404.

Puche, H. & Su, N.-Y. (2001b) Population density of subterranean termites (Isoptera: Rhinotermitidae) on tunnel formation in laboratory arenas. *Sociobiology* **38**, 523–530.

Ratcliffe, F.N. & Greaves, T. (1940) The subterranean foraging galleries of *Coptotermes lacteus* (Frogg.). *Journal of the Council of Scientific and Industrial Research* **13**, 150–160.

Robson, S.K., Lesniak, M.G., Kothandapani, R.V. & Traniello, J.F.A. (1995) Non-random search geometry in subterranean termites. *Naturwissenschaften* **82**, 526–528.

Roonwal, M. (1979) *Termite life and termite control in tropical South Asia*. Jodhpur, Scientific Publishers.

Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*, 3rd edn. New York, W.H. Freeman and Co.

Su, N.-Y. & Scheffrahn R.H. (2000) Termites as pests of buildings. pp. 437–453 *in* Abe, T., Bignell, D.E. & Higashi, M. (*Eds*), *Termites: evolution, sociality, symbioses, ecology*. Dordrecht, Netherlands, Kluwer Academic Publishers.

Tamashiro, M., Yates, J.R., Yamamoto, R.T. & Ebesu, R. (1991). Tunnelling behaviour of the Formosan subterranean termite and basalt barriers. *Sociobiology* **19**, 163–170.

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