

Research article

Foraging vibration signals attract foragers and identify food size in the drywood termite, *Cryptotermes secundus*

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Received 21 March 2007; revised 19 June and 7 August 2007; accepted 20 August 2007.

Abstract. Information gathering and communication behaviour has evolved within constraints of size, physiology and ecology of the animal. Due to these constraints, small herbivorous insects are likely to use substrate borne vibrations for information gathering and communication. Although such signals have been characterised in many types of insects, including group-living insects, they are poorly known in termites. We showed that the Australian drywood termite *Cryptotermes secundus* could determine the size of wooden blocks by using the vibrations generated during foraging. The termites behaved differently in choice experiments when artificially generated vibration signals were played compared with natural recordings, indicating that these termites can discriminate the source of the vibration as well. A T-maze experiment showed that the termites were attracted to the natural recordings of feeding termites, suggesting that vibrations are important in communication during foraging as well as food resource assessment. Combining the effects of food size preference and attraction to other termites explained differences in behaviour between artificially generated vibration signals compared with natural recordings. This study demonstrates that termites use substrate borne vibrations for information gathering and communication as predicted.

Keywords: Attraction, communication, Isoptera, signaling, vibration.

Introduction

Fast and accurate gathering of information is an important behaviour that has been selected for over evolutionary time. Clearly those individuals that find resources and detect predators and competitors most rapidly and accurately will have an advantage over slower and erroneous individuals. Of a similar importance is the communication of information in group-living species; indeed the success of group-living species is due in part to their efficiency of gathering and sharing information among foragers, such as the eusocial bees, wasps, ants and termites (Grassé, 1986; Hölldobler and Wilson, 1990; Itô, 1993; Seeley, 1995). Group living insects use several methods of information gathering and communication: visual, such as the famous honey bee dance (Seeley, 1995); chemical, such as pheromones in ants (Hölldobler and Wilson, 1990); and airborne and substrate borne vibrations.

Constraints imposed by insect size dictate that most vibrational information and communication is transmitted through the substrate form in low frequencies (Michelsen and Nocke, 1974; Bennet-Clark, 1998; Čokl and Virant-Doberlet, 2003; Virant-Doberlet and Čokl, 2004; Cocroft and De Luca, 2006). Substrate borne vibrations are well known in the eusocial Hymenoptera, such as honey bees (Michelson et al., 1986; Kirchner, 1993; Tautz et al., 1996; Nieh and Tautz, 2000; Hrncir et al., 2006) and ants (Tautz et al., 1995; Baroni Urbani et al., 1998; Hölldobler, 1999; Roces et al., 1993; Roces and Hölldobler, 1996; Hölldobler and Roces, 2000); in fact ants may not be able to detect air borne vibrations at all (Roces and Tautz, 2001).

In contrast, termite information gathering and communication signals are less well known. Worker termites

are blind and so cannot use visual signals (Grassé, 1982), like honey bees. Termite workers are known to produce only one type of pheromone other than sex pheromones, the trail following pheromone (there are different trail-following pheromones in different termite species, but each species has only one; Moore 1966; Stuart 1969), which is related to sex pheromones in the adults (Robert et al., 2004). Also, cuticular hydrocarbons have been shown to be important in colony identification in termites (Haverty and Thorne, 1989; Haverty et al., 1999). Although such chemical information is important to termites, it is insufficient to explain the complex organized behaviours observed in termites, such as building mound-nests, co-ordinating food gathering and defence. Even in foraging the trail-following pheromone can only mark a trail and not show direction, i.e. to food or to nest. Other forms of communication must be present.

Due to their size and herbivorous nature, termites are prime candidates for the study of vibrational signals. Termite soldiers produce vibrational alarm signals by drumming their heads against the substrate or shaking their bodies (Howse, 1964a,b, 1965; Kirchner et al., 1994). Only recently has a role for vibrational information gathering in foraging been inferred in termites, in order to determine food size (Evans et al., 2005; Inta et al., 2007). Other information gathering or communication roles for vibrational signals are as yet unknown. The aim of this study was to explore and demonstrate the use of vibrational signals in termite foraging using the species *Cryptotermes secundus*, a species of drywood termite (Isoptera, Kalotermitidae) endemic to tropical northern Australia (Gay and Watson, 1982). First, we explored whether *C. secundus* is able to detect wood size using vibrational signals, as previously found for *C. domesticus*. Second, we compared responses of the termites to naturally recorded signals and artificially generated signals with the same dominant frequency, to determine whether frequency is important in determining wood size. Third, we investigated attractiveness of vibration foraging signals to *C. secundus*. Finally we explain the differences in response to naturally recorded signals and artificially generated signals using the combination of wood size preferences and attraction response.

Methods

Food size preference

We determined whether *C. secundus* could detect food sizes using vibrations and if they showed food size preferences (following Evans et al., 2005). Groups of 15 worker termites were used for each replicate; the termites were from 12 colonies collected from mangroves in Darwin Harbour (12° 31' South, 130° 55' East) in northern Australia. A minimum of five colonies was used in each treatment; not all colonies were used in all treatments. The food was pine blocks of cross sectional area of 20 mm x 20 mm. Pairs of blocks were cut sequentially so that each block in a pair would be as similar as possible. The blocks were separated ca. 15 mm apart, with the freshly cut surfaces facing one another, and held together with a 15 mm 'tube' of thin LDPE plastic

Treatment

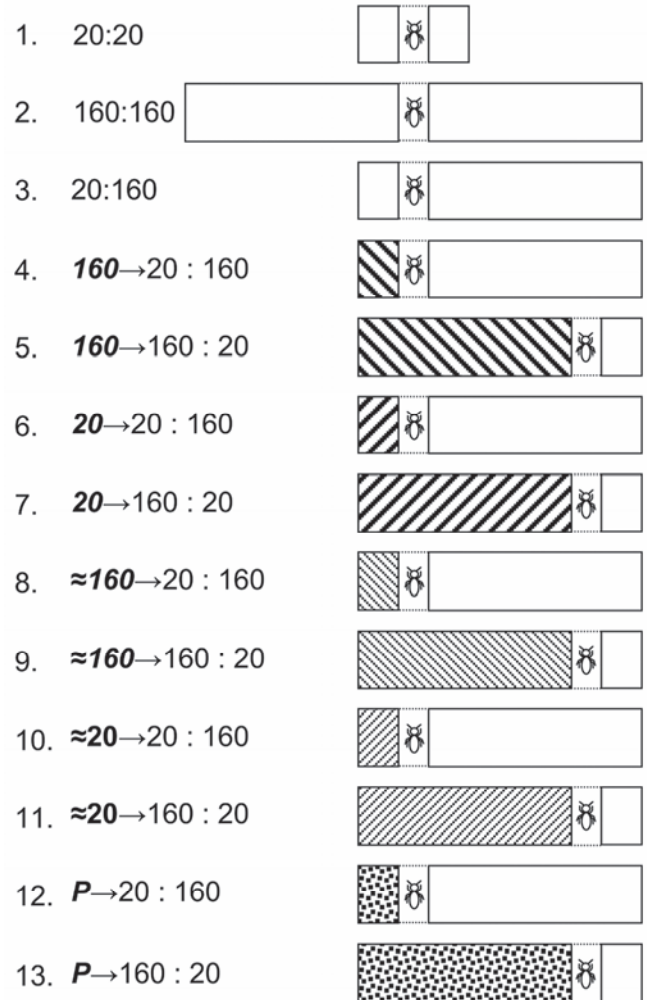


Fig. 1. Schematic of the treatments in the food size preference experiment. Treatment indicates the length of the two blocks (20 or 160 mm) and the playback signal, if any. The block excited by the signals is shaded. The termite represents the 15 worker termites in the central cell.

sheet, roughened on the base to allow for easier walking by the termites; soft plastic was used to minimize any transmission of signal. Thus the termites were exposed to (almost) identical 20 mm x 20 mm wooden surfaces and no other part of the blocks. Blocks were placed onto foam to isolate vibrationally all paired blocks in all treatments.

There were two lengths: 20 mm or 160 mm, which were arranged in three treatments (1–3, Fig. 1) (number of replicates). Treatments 1 and 2 were controls for orientation, and treatment 3 was to determine size preference.

1. 20 mm and 20 mm (12).
2. 160 mm and 160 mm (12)
3. 20 mm and 160 mm (12)

We used a procedure for recording vibration signals similar to that used by Evans et al (2005). We used groups of 15 *C. secundus* workers with seasoned, air dried *Pinus radiata* blocks, either 20 mm or 160 mm long. The recording experiment was conducted in an anechoic room and all signals were high-pass filtered above 200 Hz to reduce electrical noise. The recorded signals, typically several minutes in duration, were

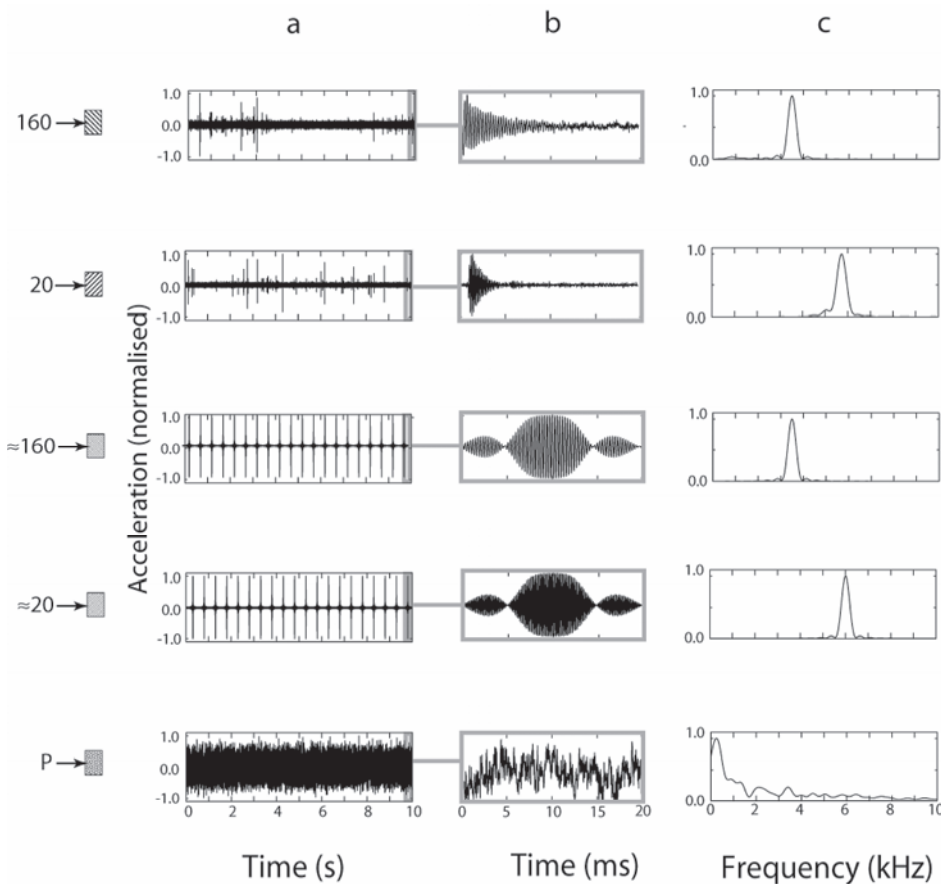


Fig. 2. Vibratory recordings of *C. secundus* workers chewing on seasoned, air dried *Pinus radiata* wooden blocks used for the playback treatments 4–13. The time series signal over (a) 10 seconds and (b) 0.20 second; and (c) the Fast Fourier Transform of the signal. Playback signal symbols to the left the graphs.

processed using a Fast Fourier Transform in MATLAB to obtain average frequency spectra, shown in Fig. 2, from which the dominant frequency was estimated. We found that the dominant frequencies of the signals were generally in agreement with signals obtained by mechanical excitation of the wood blocks and decreased with wood block length (Fig. 2) (as seen previously, Evans et al., 2005).

We played these natural signals into the blocks to test the hypothesis that the termites were determining the size of the wooden block using these signals. The blocks were attached with a screw (2 mm internal diameter, 12 mm long) to a Philip Harris vibration generator ('shaker') (model F4H31134, Leicester, England), which received the signal from a CD player (Sony D-EJ100), as appropriate to the treatment. The volume control was set to the same level for all CDs in all playback treatments. Four more treatments were created, two where signals mismatched block size (4 and 7) and two positive controls where signals matched block size (5 and 6) (Fig. 1). These treatments were, with anticipated outcomes (number of replicates):

4. 20 mm receiving the 'natural 160 mm signal' recorded from termites on a 160 mm block (dominant frequency of 3.5 kHz) and 160 mm without signal (24). The preference was expected to be neutralised.
5. 20 mm without signal and 160 mm receiving the 'natural 160 mm signal' (12). The preference was expected to be maintained.
6. 20 mm receiving the 'natural 20 mm signal' recorded from termites on a 20 mm block (dominant frequency of 5.9 kHz) and 160 mm without signal (24). The preference was expected to be maintained.
7. 20 mm without signal and 160 mm receiving the 'natural 20 mm signal' (12). The preference was expected to be neutralised.

The dominant frequency changed with block size and was an obvious feature in the natural signals (Fig. 2), so we hypothesized that this was the most important feature of the signals for the termites in determining

the size of the wooden block. To test this we generated two 'artificial' signals with frequencies matching those of the natural signals. Artificial signals were synthesised using MATLAB with pulse trains having a separation of 500 ms, and as for natural signals, the artificial signals were high-pass filtered above 200 Hz to reduce instrumental noise. We played these artificial signals into the blocks (as for natural signals) to create four more treatments that corresponded to the natural signals; two where signals mismatched with block size (8 and 11), and two positive controls where signals matched with block size (9 and 10). Treatments were, with anticipated outcomes and natural signal match (number of replicates):

8. 20 mm receiving an 'artificial 160 mm signal' generated by computer (dominant frequency of 3.5 kHz) and 160 mm without signal (24). As for treatment 4, the preference was expected to be neutralised.
9. 20 mm without signal and 160 mm receiving the 'artificial 160 mm signal' (12). As for treatment 5, the preference was expected to be maintained.
10. 20 mm receiving an 'artificial 20 mm signal' generated by computer (dominant frequency of 5.9 kHz) and 160 mm without signal (12). As for treatment 6, the preference was expected to be maintained.
11. 20 mm without signal and 160 mm receiving the 'artificial 20 mm signal' (12). As for treatment 7, the preference was expected to be neutralised.

In order to eliminate the possibility that termites were responding to vibrations in general, we generated a pink noise (i.e. static noise where energy across each frequency band is the same) signal by computer, and played the pink noise signal into the blocks (as for natural and artificial signals) to create two final treatments (12 and 13, Fig. 1), for which the preference was expected to be maintained (number of replicates):

12. 20 mm receiving a pink noise signal and 160 mm without signal (12).
13. 20 mm without signal and 160 mm receiving a pink noise signal (12)

The blocks were kept in the dark at 28°C and 80% RH for 14 days. After this period the blocks were separated and dissected, the termites counted, the number of independent tunnel origins into each block counted and the sum of the length of all tunnels measured. Tunnelling was used to determine preference because this was effort sustained over the 14 day period; termite location in blocks was not used as this could change within seconds with little effort (including during dissection of blocks). The amount of tunnelling was compared between paired blocks using 95% confidence intervals on standardized data, because normal distribution and heterogeneity of variance assumptions for ANOVA could not be met, and using the 95% C.I. is a robust method for determining ranges regardless of parametric assumptions.

Attractiveness of signal

Results from the food size preference experiment showed that the *C. secundus* workers did not behave the same way for paired natural and artificial treatments. A second effect was hypothesized to influence the choice of termites. Termites are social insects, and foraging is a group activity, so perhaps the vibrations generated by termites at the food source act as an attractant for their colony mates, as has been shown for other insects (Baroni Urbani, 1988; Tautz et al., 1998; Cocroft, 2005).

To test this hypothesis, cardboard T mazes were cut (Fig. 3a), 120 mm long and 120 mm wide, and with a breadth of the cardboard of 20 mm. The two ends of the upper cross stroke of the T were gripped by bulldog clips that were attached to Philip Harris shakers, driven by CD players (Sony D-EJ-100). The T maze was cut along the mid line, from the top to 15 mm short of the bottom end, and the two ends of the upper cross stroke were pulled ca. 0.5 mm apart, to reduce the possibility of signal transmission directly from one side of the T maze to the other, but allow easy movement by the termites from one side of the T maze to the other. Signal strength was measured at various points along the T maze, and found to increase from the termite release point to the end held by the bulldog clip connected to the shaker playing the signal, but to decrease from the termite release point to the end without the signal (Fig. 3b). This mimics the Y maze method used by Kirchner et al. (1991), who tested attraction of airborne vibrations for honey bees. There were three treatments: 1, no signal from either CD player; 2, pink noise signal from one CD player as a control for non-specific vibration; and 3, natural 160 mm foraging signal from one CD player. For treatments 2 and 3, the signal was played an equal number of times from left and right CD players.

A single termite was placed at the end of the T maze and a transparent plastic T shaped cover (creating a crevice of ca. 2 mm) was placed on the T maze. This cover reduced the air movement disliked by termites, and helped prevent the termite from walking underneath the T maze. A termite was determined to have made a choice when it had walked up the T, turned left or right and walked 30 mm towards a bulldog clip within two minutes. This time was chosen as it was ten times the period a worker termite could walk the length of the maze (viz. 12 s). If a termite had not made a choice in two minutes, it was discarded and a new individual was chosen. Tests were run until 20 termites each from six colonies had been exposed to each treatment and made a decision (a total of 601 termites were tested). No T-maze was used twice, to avoid confounding effects of any potential trail-following pheromone (Moore, 1966; Stuart, 1969). The number of discards and the number of each signal choice were tested using ANOVA and χ^2 tests.

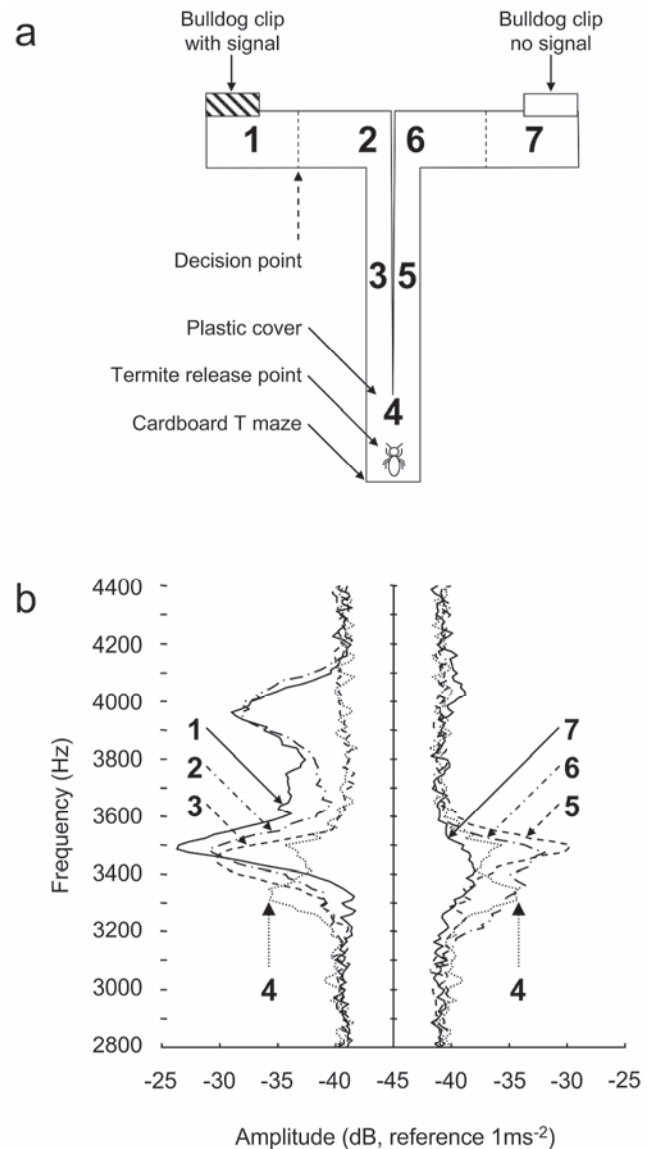


Fig. 3. The attractiveness of signal experiment. **(a)** Schematic of the T maze apparatus, the termite represents a single worker termite placed at the release point, the shaded bulldog clip represents the playback at one of the two destination ends, numbers 1 – 7 indicate recording positions with 1 = destination end with signal, 4 = termite release point, 7 = destination end without signal. **(b)** The attenuation of the signal along the T-maze shown by the change in recorded signal strength, the recording for position 4 is drawn on both sides.

Results

Food size preference

Termite survival was high (average \pm standard error, 89.3 \pm 1.0%), and did not differ significantly either between treatments ($F_{12,146} = 1.124, p = 0.345$), or colonies ($F_{11,147} = 0.883, p = 0.558$). Few termites matured into secondary reproductives (neotenics) in this experiment, typically one or two in any replicate (1.4 \pm 0.1), and so were not considered further.

Table 1. *Cryptotermes secundus* tunnelling in wooden blocks in the food size experiment. The numbers in the table are mean \pm standard deviation of the number of tunnels or the summed length of the tunnels in either wooden block. Treatment symbols as in Figure 1. N.b. for Treatment 1 both blocks were 20 mm and for Treatment 2 both blocks were 160 mm.

Treatments #	Symbol	Number of tunnels		Length of tunnels	
		20 mm	20 mm	20 mm	20 mm
1	20 : 20	1.00 \pm 0.17	1.17 \pm 0.17	6.00 \pm 1.36	6.92 \pm 1.27
2	160 : 160	0.91 \pm 0.16	1.00 \pm 0.18	4.64 \pm 1.02	5.09 \pm 1.36
3	20 : 160	0.64 \pm 0.19	2.18 \pm 0.17	2.36 \pm 0.85	9.09 \pm 1.13
4	160 →20 : 160	1.67 \pm 0.22	1.11 \pm 0.17	8.44 \pm 1.02	7.36 \pm 1.40
5	160 →160 : 20	1.00 \pm 0.21	1.42 \pm 0.15	8.33 \pm 1.90	15.33 \pm 2.07
6	20 →20 : 160	1.00 \pm 0.13	1.45 \pm 0.17	8.20 \pm 1.41	10.28 \pm 1.35
7	20 →160 : 20	0.90 \pm 0.21	1.50 \pm 0.25	4.55 \pm 1.47	11.55 \pm 1.91
8	≈ 160 →20 : 160	1.15 \pm 0.14	1.15 \pm 0.10	9.53 \pm 1.15	8.65 \pm 1.90
9	≈ 160 →160 : 20	0.67 \pm 0.19	0.83 \pm 0.21	6.71 \pm 1.92	8.00 \pm 2.20
10	≈ 20 →20 : 160	0.64 \pm 0.19	0.91 \pm 0.16	5.27 \pm 2.19	10.27 \pm 2.01
11	≈ 20 →160 : 20	1.08 \pm 0.29	1.08 \pm 0.19	7.33 \pm 1.88	8.79 \pm 1.94
12	P →20 : 160	0.75 \pm 0.28	1.25 \pm 0.14	5.25 \pm 1.85	6.50 \pm 1.22
13	P →160 : 20	0.50 \pm 0.16	1.83 \pm 0.22	2.33 \pm 0.76	10.17 \pm 1.91

The termites had no preference when presented with two (almost) identical pieces of wood, whether they were short or long (treatments 1 and 2) as the termites chewed a similar number of tunnels in either block and these were of similar length (Table 1; 95 % CI overlap with 0.5, Fig. 4). In stark contrast, termites showed a clear preference for the 160 mm block of wood in treatment 3 as the termites had chewed significantly more and significantly deeper tunnels in the 160 mm block (Table 1; 95 % CI well beneath 0.5, Fig. 5).

The results from the playback treatments were not always consistent with the hypothesis that *C. secundus* was choosing wooden blocks only on the basis of the dominant frequencies in the signals because the results for natural and artificial signals did not always correspond. In treatments 4 and 8, where the natural and artificial (respectively) 160 mm signals were played into the 20 mm blocks, the termite preference was expected to be neutralised. Instead, the preference was reversed (Table 1, Fig. 4). A mismatch in results was observed for treatments 5 and 9, where the natural and artificial (respectively) 160 mm signals were played into the 160 mm blocks. The preference was expected to be maintained, yet this was seen only for treatment 5 where it was neutralised for treatment 9 (Table 1, Fig. 4). In treatments 6 and 10, where the natural and artificial (respectively) 20 mm signals were played into the 20 mm blocks, termite were expected to maintain their preference, and they did in both treatments (Table 1, Fig. 4). However, in treatments 7 and 11, where the natural and artificial 20 mm signals were played into the 160 mm blocks, the termite preference was expected to be

neutralised or reversed, whereas it was maintained for treatment 6 and neutralised in treatment 11 (Table 1, Fig. 4).

Importantly, random noise had no effect on termite decisions, as termite preferences for the 160 mm wooden block in the pink noise treatments (12 and 13) matched that observed without any signals being played (Table 1, Fig. 4).

Attractiveness of signal

Termites were significantly more likely to make a decision when a signal was played. There was a significant difference in the number of termites discarded (i.e. those that did not make a choice) between treatments ($F_{2,15} = 8.177, p = 0.004$); significantly more termites were discarded in treatment 1 (no signal), than in the other treatments, treatment 2 (pink noise) and treatment 3 (natural 160 mm signal) (Bonferroni adjusted $p < 0.05$) (Fig. 5a).

Termites did not have a preference for left or right because in treatment 1 (no signal), a similar number of termites chose to turn left and right: a total of 61 termites turned left and 59 turned right. This was not significantly different (average number of termites per colony turning: left = 10.2 ± 0.5 , right = 9.8 ± 0.5 ; $\chi^2_1 = 0.033, p = 0.855$) (Fig. 5b). Termites were not attracted to random noise, because in treatment 2 (pink noise signal) a similar number of termites chose to walk to the signal or away from it: a total of 58 termites walked to the signal and 62 walked away. This was not significantly different (average

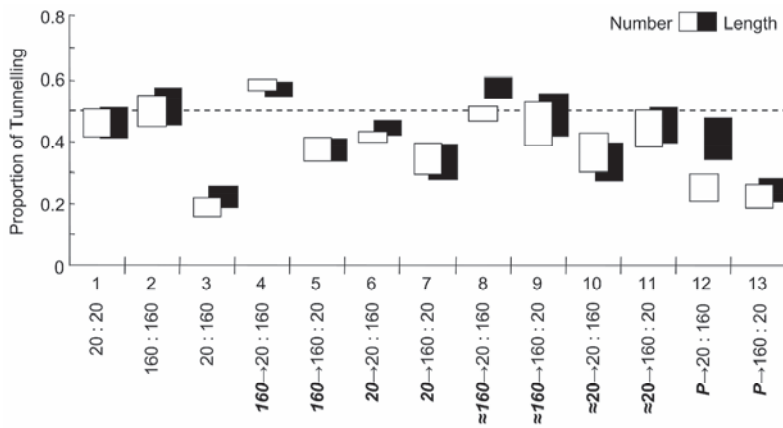


Fig. 4. The tunnelling activity of *C. secundus* workers in the 20 mm wooden block at the end of the food size preference experiment. Bars represent the 95% confidence intervals of the number of tunnels (open) and total tunnel length (closed). Treatment symbols as in Figure 1; n.b. for treatments 1 (20:20) and 2 (160:160), one block in each pair was chosen at random to calculate proportion of tunnelling activity. The dotted line indicates 50%; bars that do not overlap this line differ significantly from no preference.

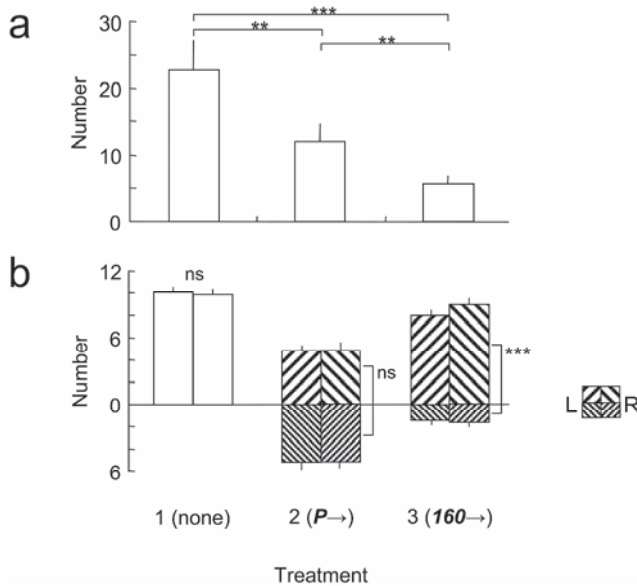


Fig. 5. Results of the attractiveness of signal experiment. **(a)** the number (average \pm standard error) of *C. secundus* workers that did not make a decision, i.e. the number 'discarded'. **(b)** the number of *C. secundus* workers that made a decision, bars above zero indicate attracted to signal and below zero indicate not attracted to signal; L = turned left, R = turned right; n.b. for treatment 1 there was no signal. Symbols as in Table 1 and Fig. 1; significance indicated as ns = not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

per colony, chose signal = 9.7 ± 1.8 , chose no signal = 10.3 ± 1.8 ; $\chi^2_1 = 0.133$, $p = 0.715$); and this was regardless of whether the signal was played on the left or the right CD player (Fig. 5b – n.b. values are halved as data are divided into left and right). In stark contrast, termites were attracted to the recordings of other termites. In treatment 3 (natural 160 mm signal), five times more termites chose to walk to the signal than away from it: a total of 101 termites compared with 19. A majority of termites in all six colonies chose to walk to the signal also, which was significantly different (average per colony, chose signal = 16.8 ± 0.8 , chose opposite to signal = 3.2 ± 0.8 ; $\chi^2_1 = 55.962$, $p < 0.001$) (Fig. 5b).

Discussion

Results from treatment 3 of the food size preference experiment indicated that *C. secundus* workers preferred to tunnel into the larger block, and must have been capable of detecting a difference in size without pacing the linear dimensions. The difference in dominant frequencies in the vibration signals recorded from the blocks suggested that these might have been the information used by the termites to distinguish the blocks. The playback experiments were designed to show whether this hypothesis was correct, using natural and artificial signals to focus on frequency, and then mismatching and matching signals with block size to either neutralise or maintain preferences. If block choice was influenced only by the dominant frequency in the signals, then the results of the paired natural and artificial treatments ought to have been the same. They were not. To account for this discrepancy, a second effect was hypothesized to influence the choice of termites: attractiveness of the natural signal. As termites are social insects, it seemed possible that termites use vibrations to find their colony mates. This hypothesis was supported in the T maze experiments, which demonstrated that worker termites will explore natural but not artificial signals.

The results of the food size experiment can be reconsidered with two effects: the preference for larger food, and attraction to other foraging termites. This can be illustrated with an example, e.g. treatment 4 in the food size preference experiment (natural 160 mm signal was played into a 20 mm block paired with a 160 mm block without a signal). The termites should perceive both blocks to be similar in size, due to the dominant frequency of 3.5 kHz in the signal, but should prefer the 20 mm block because from it emanates the natural signal that indicates the presence of other conspecifics. In fact termites did prefer the 20 mm block in treatment 4.

Table 2 shows the expected results for all treatments when considering these two effects, and also the observed results, for tunnel number and tunnel length. The expected choice matches the observed result in seven of

Table 2. The expected and observed foraging choices of wooden blocks by *Cryptotermes secundus*, as influenced by food size and social attraction effects. A dash indicates that either no choice was expected or observed; the question mark in treatment 6 indicated the sum of the effects was unknown. Observed choice from Figs. 4 and 5, treatment symbols as in Figure 1.

Treatments #	Symbol	Expected choice			Observed choice	
		Food size Effect	Attraction Effect	Sum of both Effects	Tunnel number	Tunnel length
1	20 : 20	–	–	–	–	–
2	160 : 160	–	–	–	–	–
3	20 : 160	160	–	160	160	160
4	160 →20 : 160	–	20	20	20	20
5	160 →160 : 20	160	160	160	160	160
6	20 →20 : 160	160	20	?	160	160
7	20 →160 : 20	–	160	160	160	160
8	≈ 160 →20 : 160	–	–	–	–	20
9	≈ 160 →160 : 20	160	–	160	–	–
10	≈ 20 →20 : 160	160	–	160	160	160
11	≈ 20 →160 : 20	–	–	–	–	–
12	P →20 : 160	160	–	160	160	160
13	P →160 : 20	160	–	160	160	160

the nine playback treatments in which a clear expected choice could be determined. The exceptions were treatments 8 and 9, both of which used the artificial 160 mm signal, suggesting that our signal synthesis was inadequate. Treatment 6 was the only playback treatment in which an expected choice could not be determined, because the two effects predicted opposite choices. We had no expectation as to whether termites would place greater importance on food size or social attraction, but our results suggest the former.

The results from this study demonstrate that the *C. secundus* termites were using vibrational signals to evaluate the size of their wooden food and the presence of other termites. That termites were using vibrational signals is not unexpected, because termites are small, herbivorous insects, and substrate-borne vibrational signals are very suitable for information gathering and communication in such animals. For example, substrate-borne vibration signals communicate presence and attraction between group members, such as mothers and offspring or siblings, in many sucking bugs (Homoptera and Hemiptera), sawflies (Hymenoptera), and caterpillars (Lepidoptera) (Carne, 1962; Claridge, 1985; DeVries et al., 1993; Travassos and Pierce, 2000; Cocroft, 2001, 2005; Čokl and Virant-Doberlet, 2003; Cocroft and Rodríguez, 2005), alarm and defence in sap-sucking bugs (Cocroft, 1996), and in caterpillars (Yack et al., 2001; Fletcher et al., 2006). Social Hymenoptera are also known to use substrate-borne vibration signals, particularly for foraging behaviours. Ants recruit workers to foraging sites using vibrations signals (Baroni Urbani, 1988; Roces et al., 1993; Roces and Tautz, 2001; Roces and Hölldobler, 1996), and dancing honey bees, which are workers recently returned from foraging flights, recruit foragers to their dance using vibration signals (Michelsen

et al., 1986; Kirchner, 1993; Kirchner et al., 1991; Tautz et al., 1996; Nieh and Tautz, 2000).

The attractiveness of the vibration signal from termites chewing can be interpreted in a natural context. Although drywood termites live inside a single piece of wood, this piece of wood may be large, such as a branch or even a tree. Drywood termites do not form a distinct nest inside their food; rather they live in the tunnels and hollows created by their feeding. The reproductives roam, lay eggs and care for young only in one part of the colony, but this may change over time (Noirot, 1970; Gay and Watson, 1982; Korb and Schmidinger, 2004). Thus, worker termites may have difficulty in finding the centre of the colony and since they live within the hollow created by their own feeding, they would be surrounded by their own scent. Vibration signals are less persistent and would be a reliable indication of the presence and location of other colony members. It may be that drywood termites live in an environment better adapted for substrate borne vibration signals relative to other herbivorous insects. Living plant tissue, such as leaves and stems, and inclement weather, such as wind and rain, act to dampen signals or add noise, and so reduce the range of any communication (Michelsen et al., 1982; Cocroft and Rodríguez, 2005), compared with the relatively rigid (at least along the grain) and constant environment within dry wood.

Termites do use other information sources and communication methods, such as chemicals. Termites use cuticular hydrocarbons to identify individuals from their own and other colonies (Haverty and Thorne, 1989; Haverty et al., 1999), which have genetic and environmental influences (Florane et al., 2004; Uva et al., 2004; Dronnet et al., 2006). Trail-following pheromone in workers (Moore, 1966; Stuart, 1969; Peppuy et al.,

2001), which seem to have evolved from sex pheromones (Robert et al., 2004; Laduguie et al., 2004) are clearly important in foraging behaviour. Faeces have also been implicated in a trail marking role (Souto and Kitayama, 2000). The trail-following pheromones are found in subterranean termites, which unlike drywood termites, have the capacity to tunnel in soil and so forage away from their nests. Trail-following pheromones have no polarity, i.e. they cannot indicate direction to food or to the nest. For ants it is the geometry of the trails that give polarity, thus they use an existing trait without requiring a separate, special signal (Jackson et al., 2004). A similar situation is plausible for termites, in which the foraging vibration signals could provide polarity as they would emanate only from foraging sites. The results from this study on a drywood termite are suggestive, but similar signals and attractiveness are yet to be discovered in subterranean termites. This may be possible, given that vibrational alarm signals are known from termites across their phylogeny and with diverse nesting and foraging habits (Howse, 1964a, 1965; Stuart, 1969; Kirchner et al., 1994; Connétable et al., 1999; Röhrig et al., 1999), and the similar findings on cockroaches (Howse, 1964b; Shaw, 1994).

Several other questions arise from this study. This work did not attempt to elucidate the details of the signals, other than the dominant frequency. Although the dominant signal appears to be important in helping to determine wood size, it is unlikely to be the only important feature of vibration signals as demonstrated by the attractiveness of natural signals. Understanding which component or components of the signal identify its termite origins may aid in understanding the cause of attraction. A comparison of the time series plots of the natural and artificial signals (Fig. 2b) suggest that the temporal structure of the signal will be important. As the above discussion on trail-following pheromones suggests, we do not know how signals vary between species in different termite genera or families, whether different species can distinguish heterospecific signals, and so forth. These suggestions raise testable hypotheses, viz. sympatric termite species that compete for the same food source may be more capable of distinguishing vibrational signals from different species, compared with those that do not compete. Or are termites able to detect predators or competitors, as demonstrated for caterpillars (Yack et al., 2001; Castellanos and Barbosa, 2006; Fletcher et al., 2006)? Previous work (Evans et al., 2005) showed that a congeneric species, *Cryptotermes domesticus*, prefers food of smaller size. Assuming that these two termites use the same mechanism for determining food size, why do they have opposite preferences – could they be explained by ecological factors? Given the paucity of alternative mechanisms for information gathering and communication, it would appear that there is considerable scope for investigations into vibration signals in termite communication and behaviour.

Acknowledgements

We thank Aaron Barrett, Patrick Gleeson and Wendy Whitby for their help with bioassays, and the financial support of the Australian Research Council under the Discovery Project Scheme. The experiments performed in this study comply with the current laws of Australia.

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