WHAT DO VIBRATIONS HAVE TO DO WITH TERMITES' FOOD CHOICE?

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ABSTRACT. It has been shown previously that termites are sensitive to vibrations, using them as a communication channel. However, their ability to use vibrations in assessment of food structures is little understood. Here we present timber of differing quantities to two drywood termite species, *Cryptotermes domesticus* and *Cr. secundus*. We also expose the termites to vibration signals produced as a by-product of their feeding, and to food sources with altered effective material properties. We show here that both species have a food size preference, which is determined by vibrations. We also show that *Cr. secundus* is able to discriminate material properties. Although the exact characteristics in the vibration signals they utilise are yet to be fully identified, these observations reveal previously unexplored aspects of termite foraging decision-making, which might help to minimise their economic impact.

1. BACKGROUND

Termites are important insects, both economically and ecologically. It has been estimated that roughly one in three houses in Australia would be attacked by termites at some time during their life [1]. The total cost due to termite damage in Australia was estimated recently to be A$780 million per annum [2]. According to another estimate [3], the cost of structural damage caused by termites amounted, in the USA alone, to US$11 billion. Termites are also among the most important herbivores in Australia [4], and play an important role in engineering soil properties [5]; it has been estimated that termites contribute up to 5% of the annual global atmospheric methane [6].

Observations indicating that termites use vibrations in conspecific communication were made quite some time ago, both naturally [7, 8], and artificially, induced [9-12]. Vibratory signals are well known to be a useful means of communication amongst animals. It has been estimated that 80% of arthropod species use substrate vibrations in some way [13]. There are many reasons why termites specifically might use vibratory signals. Non-reproductive castes of termites are blind and have a number of mechanoreceptors. The subgenual organ, located in their tibiae, is the most sensitive to vibrations, being able to detect displacements down to 0.2 nm [14, 15]. Also, considering their highly social and complex societies, the use of vibratory communication would be highly beneficial for rapid transmission of information among termites.

Perhaps the most easily observed vibratory communication is that of the alarm signals produced by the termite soldiers. They repeatedly and forcefully strike the substrate with their heads in response to an intrusion [8, 11, 12, 16, 17] or detection of a potentially toxic pathogen [18]. If there is sufficient soldier alarm activity, the termite workers will retreat to a more central region of their nest [8].

More recently, vibratory signals have been associated with foraging activity of termites, e.g. [19, 20]. The vibratory signals produced during feeding have been partly characterised (e.g. [19]) and could be used for termite detection [21-23]. Patterns of development of reproductives (kings and queens) and survival in termite colonies, for a range of species, vary with changes in resource availability [24, 25]. This demonstrates a complex allocation of biological strategies in response to access to resources, despite the fact that the termites were not able to pace out the wood and did not tunnel to the wood surface. This prompted speculation that the mechanism behind this food assessment might be vibratory in origin [24]. If this speculation proves correct, what key measures do they use to assess the food type and size? Termites have a relatively simple nervous system, with the entire cerebral ganglia of most termites occupying a volume of the order of 0.1 mm^3 [26]. Thus it might be expected that they rely on relatively simple features of the vibratory signals.

In this paper, evidence is presented firstly to establish that termites can assess their food using vibrations, and then some key measures they might apply in this assessment will be explored. This is demonstrated by way of bioassays, whereby the foraging termites are given a choice between two potential food sources, one of which is of a standard size (160 mm X 20 mm X 20 mm) and the other is varied appropriately. The first series of assays was designed to test the hypothesis that vibrations are the mechanism behind food size assessment of termites, by exploiting their innate preferences for food size. The second was designed to further investigate possible key features in the vibratory signals that the termites use in their assessment by attempting to manipulate their behaviour using blocks of composite materials.

2. MATERIALS AND METHODS

Termite and wood species: Two drywood termite species were used in the bioassays and the recordings: *Cryptotermes domesticus* and *Cr. secundus*, both obtained from mangrove trees near Darwin, NT (012°31' S, 130°55' E) respectively. All bioassays were conducted in a controlled environment at 28°C and 80% RH. During signal recordings, the temperature was maintained at 28°C but the humidity was not controlled. All wood used in the studies were of seasoned untreated *Pinus* *radiata*, fashioned into rectangular blocks such that the grain was aligned parallel to the main axis.

Vibratory recording: Fifteen pseudergate (worker) termites were housed in a small chamber drilled into blocks 160 mm in length, held loosely in the middle by a clamp with foam rubber jaws (Figure 1). An accelerometer (Brüel & Kjær 4370, Nærum, Denmark. S/N:1360490) was stud-mounted to the base, which was connected via a charge amplifier (Brüel & Kjær 2635, Nærum, Denmark) to the sound card of a desktop computer running the software package CoolEdit (Syntrillium Software Corporation, Phoenix, AZ). The recordings were performed inside an anechoic chamber.

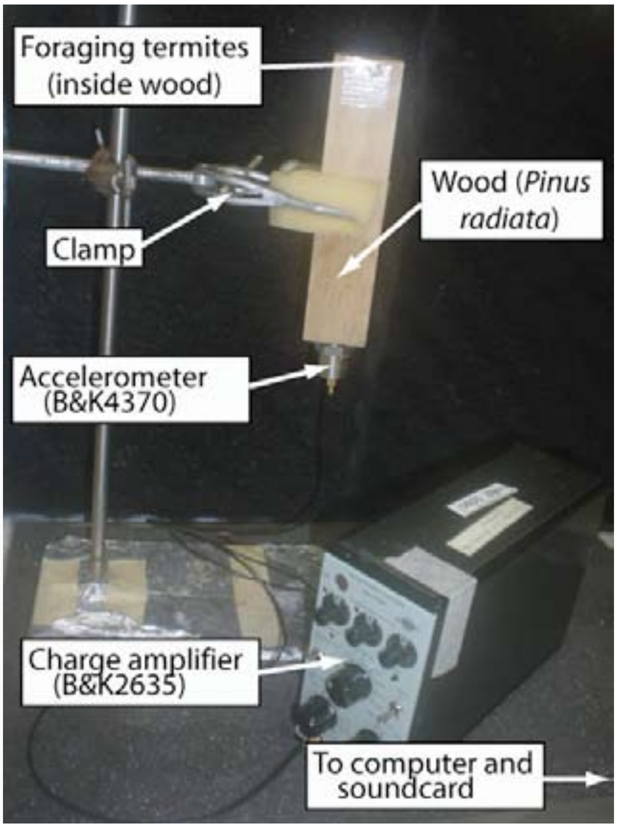

Figure 1: The set-up used to record the vibratory emissions given by drywood termite workers (subgenus: *Cryptotermes*) foraging at one end of a block of wood. Fifteen drywood worker termites fed on one end of a wooden block, while an accelerometer recorded the vibratory signals at the opposite end.

Feeding choice bioassays: For both studies, we needed to determine the feeding preference of the termites. As an extension of previous termite foraging experiments (e.g. [24]), blocks of wood having a constant, square, 20 mm X 20 mm cross-section were cut contiguously from the same timber source, and were presented directly opposite each other, separated by a 20 mm X 20 mm X 20 mm sealed cubic cell with walls of clear thin plastic (LDPE) (after [27-29]). Fifteen termites of either species were inserted into the central chamber. They fed on the wood for a period of fourteen days. As drywood termites tend to make relatively constant cylindrical tunnels, the total length and number of tunnels was recorded, to obtain a measure of tunnelling activity, and the position of individual termites (i.e. on either block) was noted daily for the first five days of the experiment. Together these observations were taken as a gauge of feeding preference [27]. The blocks were placed on vibration damping foam rubber, alternated spatially, to reduce broad environmental effects, and the orientation of the blocks was rotated by 180° after observation of the termites on each of the first five days.

Food size preferences: There were a total of four treatments (Figure 2), with number of replicates as specified in the Results section. All treatments had a 160 mm long block of wood on one side as a reference, and both species, *Cr. domesticus* and *Cr. secundus*, were used. Treatment 1, two 160 mm blocks (160:160), was a control. Treatment 2, having a 20 mm 'test block' opposite the 160 mm 'reference block' (20:160), was designed to test the natural food size preference of the termites [27-29]. Treatments 3 and 4 involved playback of vibratory signals through 20 mm blocks, which were fixed onto aluminium bars with a single wood screw, and driven by a shaker (Phillip Harris vibrator shaker, Leicester, England) *via* a CD player (Sony D-EJ100, Tokyo, Japan). The signal played in Treatment 3 (pink) was pink noise, in the band 0-20 kHz, synthesised using MATLAB. This was designed to act as treatment for a non-specific source of vibrations. Pink noise was chosen in order to emulate the noise profile of the instrumentation used in the vibratory recordings, which was largely due to instrumentation noise resulting from the high levels of amplification required. Treatment 4 (160 natural) played back the recordings made of the particular termite species feeding on a 160 mm block of wood [27, 29]. Although the signals used in playback were recorded from 160 mm lengths of wood, the signals perceived by the termites during playback will be modified by the properties of the playback system.

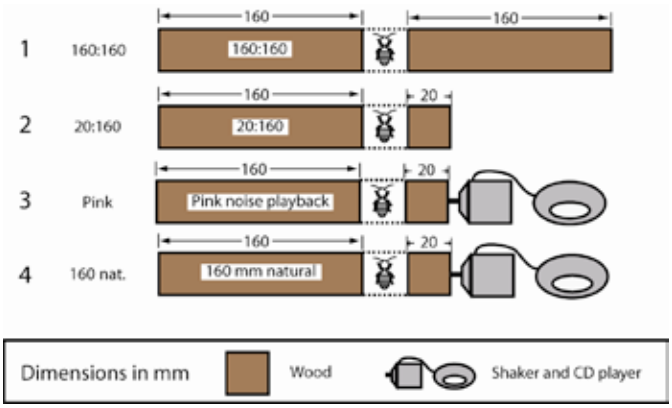

Figure 2: Schematic of set-up to test food size preferences in the drywood termite species *Cryptotermes secundus* and *Cryptotermes domesticus*. All treatments were opposite blocks, having a constant, square, 20 mm X 20 mm cross-section, with a 160 mm long block of wood on one side as a reference. The two playback experiments (pink noise and 160 mm natural foraging signals) were played back through a 20 mm block.

Ability to discriminate materials: This study comprised five treatments (Figure 3). Again, all treatments had a 160 mm long block of wood on one side as a reference. However, in this study, only the species *Cr. secundus* was used. The test block in Treatment 5 (discontinuity) consisted of a 20 mm and 140 mm contiguous block glued together to provide an artificial impedance boundary in the block. Treatments 5-9 were designed to test key measures in the vibratory signals the termites might use: that of the fundamental frequency, the mass or possibly the damping (or impedance) properties of the block [28]. This was done by glueing lengths of aluminium (having a high speed of sound and very low damping) or EPDM rubber (very low speed of sound, very high damping), each with constant 20 mm X 20 mm square cross-sections, on to a 20 mm wooden block.. The test blocks used in Treatments 6 (aluminium frequency) and 8 (rubber frequency) were designed such that they had approximately the same fundamental frequency as the reference block, using, respectively, lengths of aluminium and rubber. Treatments 7 (aluminium mass) and 9 (rubber mass) were designed to have the same mass as the reference block, again with aluminium or EPDM rubber. The accelerance spectra of the beams were measured to ensure these properties were, in fact, altered accordingly [28].

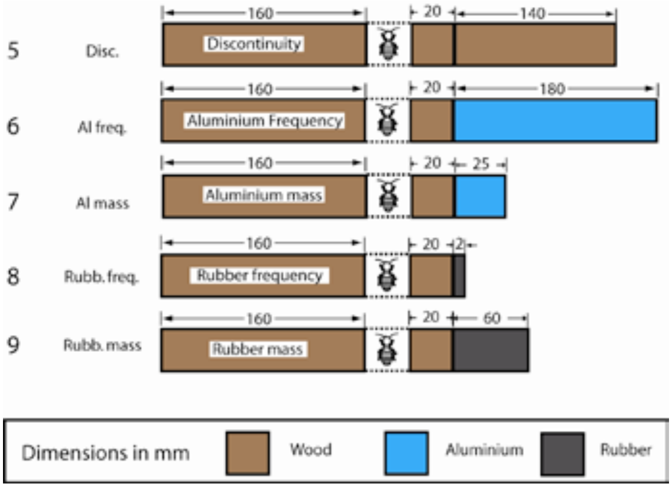

Figure 3: Schematic of set-up to assess the ability for discriminating materials of potential food structures for the species *Cryptotermes secundus*. All treatments were opposite blocks, having a constant, square, 20 mm X 20 mm cross-section, with a 160 mm long block of wood on one side as a reference opposite a composite test block with a 20 mm long block of wood with some other material attached to alter the effective vibratory characteristic of that food structure.

3. RESULTS

Recordings: the measured foraging signals (Figure 4) are similar to those of mechanical impulses; the dominant frequencies of the acceleration spectra, over time-averaged data taken from a series of peaks, are very similar to those obtained by striking the wood with a pair of tweezers, suggesting that the feeding signals are excitations of the substrate structure, and not produced by the termites themselves. However, this does not rule out vibratory communication using transient vibrations. The peak force, obtained from the measured acceleration levels, was *ca.* 20 mN. The motion of the beam, deduced from the measured acceleration spectra, appears to be that of a free-free beam mass loaded at one of the antinodes.

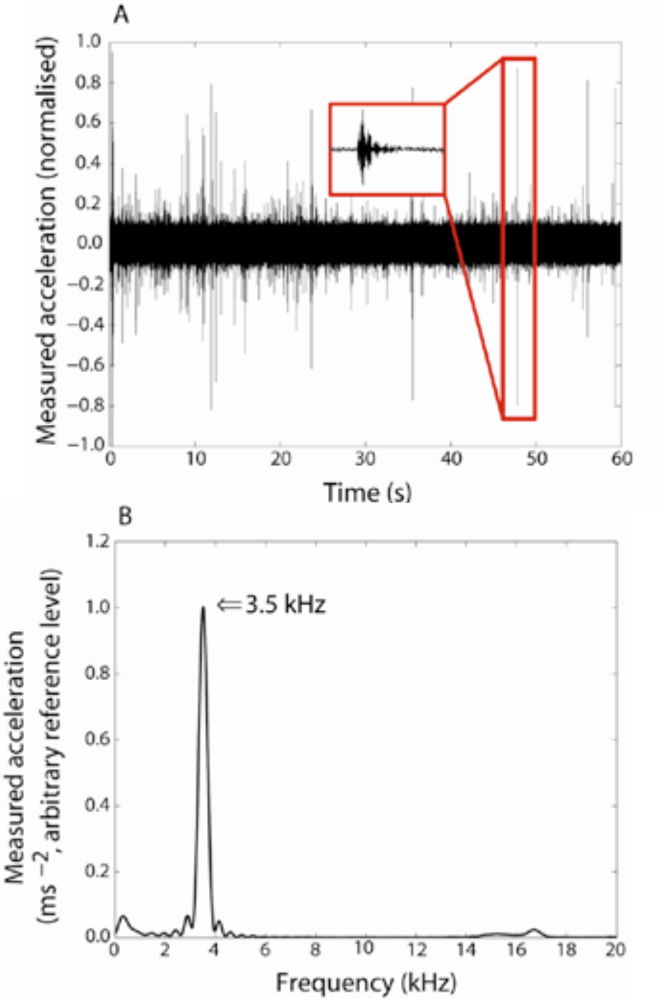

Figure 4: Measured acceleration of *Cr. secundus* feeding on a 160 mm length of wood. A shows the acceleration varying over time as a series of impulses, including a time-enlargement of a single pulse (window size: 10 ms). B shows the power spectrum average of the pulses, with a peak at approximately 3.5 kHz for this size of wood.

Feeding bioassays: Because the tunnel length data were not normally distributed, the bias introduced by outliers between replicates was reduced by examining the proportion of the amount of tunnelling in the 160 mm wooden reference block, taken, in each replicate, as the amount of tunnelling in the reference block divided by the total amount of tunnelling. The mean of the observed number of termites on the 160 mm block, for each replicate, on each day, was taken as a single measure of position for each treatment.

Food size preferences: For both species, there was no significant preference for blocks of wood of the same size (Treatment 1 (160:160)). For *Cr. secundus* (as a mean proportion in the 160 mm block, total tunnel length ± s.e., number of tunnels ± s.e., position ± s.e. (N = number of replicates)) (0.510 ± 0.111, 0.514 ± 0.088, 0.520 ± 0.041 (N = 12)), Cr. domesticus, (0.439

± 0.086, 0.432 ± 0.068, 0.489 ± 0.028 (N = 16)) Figure 5). However there was a significant effect of food size (Treatment 2 (20:160), *Cr. secundus* (0.805 ± 0.072, 0.812 ± 0.058, 0.759 ± 0.034 (N = 11)), *Cr. domesticus* (0.402 ± 0.053, 0.329 ± 0.038, 0.368 ± 0.015 (N = 44))). Most interestingly, despite this significance, the two species had *opposite* food size preferences.

In testing for a response to the playback of vibratory signals, the preference of *Cr. secundus* in Treatment 3 (pink) was altered to show no significant preference (0.544 ± 0.109, 0.583 ± 0.088, 0.473 ± 0.033 (N = 12)), as for *Cr. domesticus* (0.370 ± 0.068, 0.357 ± 0.061, 0.395 ± 0.022(N = 32)). Playback of the respective species feeding on 160 mm long blocks (Treatment 4) had the effect of swapping the preference for both species: for *Cr. secundus* (0.425 ± 0.070, 0.417 ± 0.052, 0.401 ± 0.014 (N = 24)), and for *Cr. domesticus* (0.698 ± 0.064, 0.656 ± 0.056, 0.539 ± 0.029 (N = 32)).

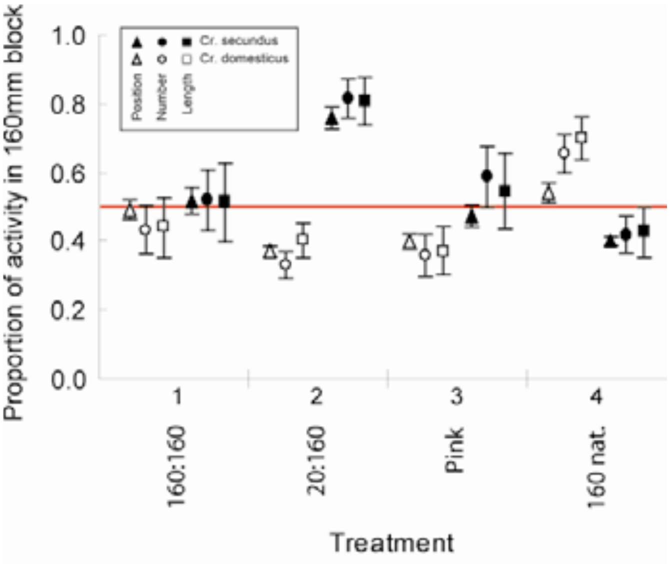

Figure 5: Proportion of total tunnelling activity (mean ± standard error) in 160 mm long reference wooden blocks for the two species of drywood termite to determine their food size preferences. Triangles denote the observed position of the termites, circles the number, and squares the total length, of tunnels. Treatments 1 (160:160mm control) and 2 (20:160 mm) were designed to test the natural foraging preference of the termites. Treatments 3 (pink noise playback) and 4 (recorded 160 mm playback) were designed to test the effect of vibrations, played back to the termites, on their preference. The red line at 0.5 is a reference indicating the ordinate position for no preference for either block.

Ability to discriminate materials: A discontinuity in the wood (Treatment 5) appeared to have no effect on the feeding preference of *Cr. secundus* (0.406 ± 0.031, 0.406 ± 0.031, 0.406 ± 0.031(N = 12)). However *Cr. secundus* preferred the 160 mm reference block for the aluminium frequency treatment (Treatment 6, (0.806 ± 0.019, 0.806 ± 0.019, 0.806 ± 0.019 (N = 12))) and the aluminium mass treatment (Treatment 7, (0.878 ± 0.011, 0.878 ± 0.011, 0.878 ± 0.011 (N = 12))) as well as for the rubber frequency treatment (Treatment 8, (0.806 ± 0.044, 0.806 ± 0.044, 0.806 ± 0.044 (N = 12))) and the rubber mass treatment (Treatment 9, (0.642 ± 0.060, 0.642 ± 0.060, 0.642 ± 0.060 (N = 12))).

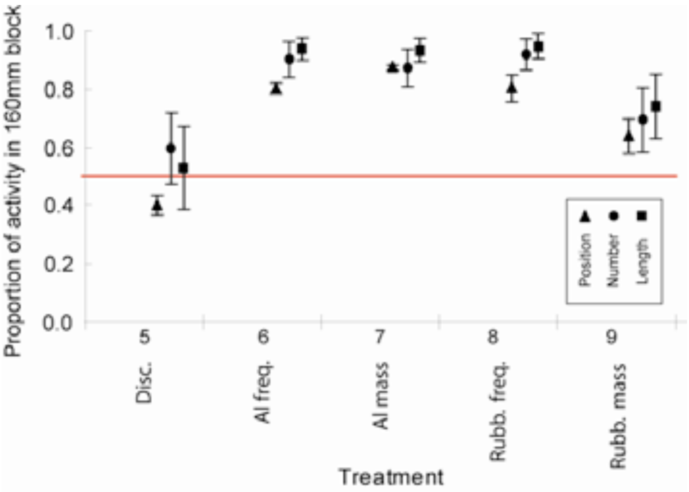

Figure 6: Proportion of total tunnelling activity (mean ± standard error) in 160 mm long reference wooden blocks to assess the ability to discriminate materials for the drywood termite species *Cr. secundus*. Triangles denote the observed position of the termites, circles the number, and squares the total length, of tunnels.

4. DISCUSSION

The studies presented here are meant as illustrative examples only, and more precise tests of the role of vibrations in food assessment by termites would be very useful. However, the results in the study on food size preferences (Figure 5) show definitively that termites use vibratory signals to make foraging choices of potential food structures. The results in the follow up study, to attempt to determine key measures in vibratory signals (Figure 6), show a perhaps surprising degree of sophistication, considering the simplicity of the nervous system of these organisms.

The two species used here, *Cr. secundus* and *Cr. domesticus*, were chosen to illustrate their contrasting foraging strategies. The former had a preference for larger, while the latter preferred smaller, blocks of wood. This may be because of their difference in life history: *Cr. domesticus* is an invasive cosmopolitan pest adapted to utilising small to large timber items, while *Cr. secundus* is a non-invasive native that occupies trees of variable size. It is plausible that the social nature of termites is a factor in the choice of potential food, especially under the experimental conditions presented here; the worker termites are in an unfamiliar environment, separated from the majority of their nest-mates [29].

The reaction of both termite species to the playback signals (Treatments 3-6) was similar. Playback of pink noise and foraging signals obtained in 20 mm wood block through the 20 mm wood block appeared to have no effect on their natural food choice preference (i.e. *Cr. secundus* preferred larger, while *Cr. domesticus* preferred smaller, wood blocks) or slightly shifting their preference towards the 20 mm block. However, playback of foraging signals obtained in 160 mm wood block through the 20 mm block reversed their natural food choice preference (i.e. *Cr. secundus* now prefers the smaller, while *Cr.*

domesticus prefers the larger, block). These results suggest that both termite species perceived the 20 mm wood block that was driven by the foraging signals obtained in 160 mm wood block as larger than 20 mm.

The feeding preferences of *Cr. secundus* indicate that they are able to determine some aspect of the material properties of their food structures in Treatments 7-11. These termites do not appear to use the fundamental frequency, or total mass, as the only measures in determining their preference for a potential food structure. However, the key characteristics in the vibratory signals they use have not yet been fully studied and identified. By applying similar methods described here, it would be possible to test if the termites make use of information obtained from, for example, the damping or impedance mismatch properties of the food that they eat [28].

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