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TERMITES THRIVE BY USING VIBRATIONS

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Termites are notoriously cryptic: infestations in houses are often discovered when an apparently intact timber object collapses, the archetypal 'falling through the floor boards'. This behaviour is adaptive because remaining undiscovered is the termite's primary defence against predators. However, being cryptic severely limits the ability of termites to explore their environment and assess potential food sources. Despite being blind and hidden, termites can assess a piece of wood swiftly after contacting only a small part of it (sometimes as little as a few square millimetres). Although termite soldiers have been known to produce vibratory alarm signals to warn conspecific workers, it is not until our sustained research over the last 10 years that termites have been shown to use vibrations as a principal tool for communications, making foraging decisions and detection. In this paper, some of our recent discoveries on the use of vibrations by termites will be discussed. These include the discovery of (a) two drywood termite species, *Cryptotermes* (*Cr.*) *domesticus* and *Cr. secundus*, using vibration signals produced as a by-product of their feeding to assess food size; (b) the ability of *Cr. secundus* and *Coptotermes* (*Co.*) *acinaciformis* to discriminate material properties based on vibration signals; and (c) the amazing ability of the subterranean termites *Co. acinaciformis* to distinguish unloaded wood from loaded wood. Food size is just one factor termites consider when foraging; competitors and predators are also important factors. Our results show that *Cr. secundus* worker termites are able to discriminate their own species from the subterranean species, *Co. acinaciformis*, by eavesdropping on their competitors, while *Co. acinaciformis* can detect and avoid one of their main predators, ants of the species *Iridomyrmex purpureus*, using only vibrations caused by ants walking.

Keywords: termites, eavesdrop, vibration cues, predators, competitors

1. Introduction

Termites are important insects both in economic and ecological terms. Although it is difficult to assess the true economic impact that wood-eating termites cause in Australia and other countries, pre-purchase home inspection statistics compiled by the Archicentre of the Australian Institute of Architects have found that 35% of all homes sold have some form of termite, borer, dry rot or timber fungus problem[1]. The cost of pest treatment and repair of damage in Australia was estimated by the Archicentre in 2006 to be A$910 million per annum[1], and many times higher in other countries (such as the USA and Japan [2]). According to an estimate in 2003 [3], the annual worldwide cost of structural damage caused by termites amounted to US$22 billion. Similarly, it is difficult to assess the total ecological importance of termites. They are found in all tropical to warm temperate latitudes, and are major herbivores and decomposers, dominating this functional group in tropical savannahs and arid landscapes. They are a major food source for many animals; even mammals have evolved to be termite-hunting specialists (e.g. numbats, pangolins and aardvarks). This importance and their success is due in part to their sociality: termites live in colonies of thousands to millions of individuals. They have many castes with specialised behaviours [4]. Termites have poorly developed anatomical defences and so live cryptically, in tunnels in the soil or wood. Their cryptic nature, combined with their cellulose diet, has earned them a notorious status as pests. Yet, little is known about how termites locate and assess their food sources; still less is known about communication and task allocation during foraging.

Insect chemical signals, especially those from ants, have received much attention over the last 30 years. Ants have many pheromones, used to communicate alarm, mark foraging trails, recruit fellow workers to an activity, indicate reproductive or other physiological state, and indicate colony identification [5]. The reliance by ants on pheromones is indicated by the number of glands they have evolved to produce them: 39, compared with 14 in wasps and 21 in honeybees [6]. In contrast, termites have few pheromones. Like ants, termite workers produce a trail following pheromone, which is derived from the sex pheromones in the reproductive adults [7]. Also like ants, termites use pheromones for colony identification [8, 9]. Yet neither of these can explain complex organised behaviours [10-13].

Many insects use vibration signals for communications in sexual, defensive and foraging behaviours [14], such as the familiar sounds of air-borne mating signals in crickets, kaytidids and grasshoppers [15-17]. Many small insects utilise substrate-borne vibrations for communication because of the small size of their receptor organs and their living environment [18]. It was discovered in the 1960s that termite soldiers communicated alarm through the substrate by drumming their heads or shaking their bodies [17, 19-23]. Termites are well equipped for sensing such vibrations, with chordotonal (Johnston's) organs at the antennae base and the subgenual organs are in the tibia of the leg. Campaniform sensilla are often found nearby and are also used for substrate vibration detection [20, 21]. Termites also have trichoid sensila, a long hair that is found all over the body, which usually detect airborne vibrations.

Many studies demonstrated that termite workers responded to vibrational alarms produced by termite soldiers [24-26]. However no other communication possibility for vibrations was considered until 1994 when Lenz [27] reported on alternative reproduction strategies adopted by drywood termites, *Cryptotermes spp.*, in response to different amounts of food. The termites responded adaptively but the manner in which the termites were exposed to the food prevented them from measuring it in any physical manner. Lenz suggested the use of "acoustic signals as one likely option for the termites to have quickly gained some information about the quantity of their food source"[27].

Our research was the first to demonstrate the ability of termites to detect vibrations and to use the information contained in the vibrations caused by foraging to assess food size [28, 29] and to assess the quality of the food [30]. In addition, we have shown that termites utilise clay to build structural support to increase foraging resources[31]. Food size and food quality are not the only determining factor for foraging as the presence of competitors and/or predators is also an important factor considered by termites. Termites can be found living and foraging in the vicinity of competitors and/or predators; how they detect and avoid their competitors/predators is not known. In this paper, results of our recent research on the role of vibrations in termites eavesdropping to avoid competitors/predators are presented to show that *Cr. secundus* workers eavesdrop on vibrations produced from feeding by their competitor, *Co. acinaciformis*[32] and that *Co. acinaciformis* detects their main predator ant *Iridomyrmex* (*Ir.*) *purpureus* using only vibrations of the ants' footsteps[33].

2. Termites use vibrations to eavesdrop on competitors

The mechanism for avoiding competitive exclusion in termites was not known until our study to test the hypothesis of eavesdropping as a possible mechanism [32]. Drywood termites appear to be especially vulnerable: *Cryptotermes* colonies originate in branches from winged reproductives, and their queens do not enlarge their ovaries or abdomens, and so lay few eggs, thus their colonies are usually small (typically 200-300 individuals). *Cryptotermes* colonies contain few (sometimes only one) defensive soldiers, which have relatively small jaws instead relying on their phragmotic heads to block tunnels. Also, drywood termite colonies remain within a single tree or piece of wood as they are unable to tunnel through soil, thus preventing escape. In comparison one of their main interspecific competitors is *Coptotermes* are strong competitors, a dominant subterranean wood-eating termite in Australia; they infest more than 85% of trees [34]. They originate from winged reproductives also, but *Coptotermes* queens in their ground based colonies become physogastric, producing colonies of one million or more individuals, with tens of thousand of aggressive soldiers with long biting mandibles and sticky glue secretions. *Coptotermes* colonies forage on up to 20 trees simultaneously, they enter trees through their roots and 'pipe' the tree by eating the inner heartwood up to the branches. Despite the apparently overwhelming competitiveness of *Coptotermes*, *Cryptotermes* colonies can co-exist in *Coptotermes* infested trees, as shown in Figure 1 and therefore must have evolved strategies to avoid Coptotermes [34].

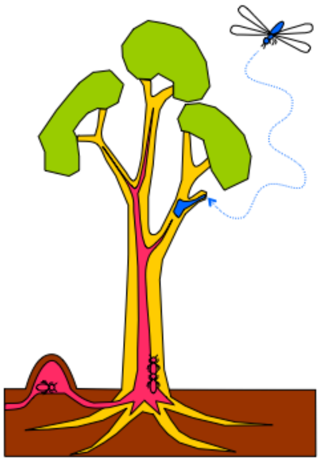

Figure 1: Schematic diagram of a tree infested by a colony of *Cryptotermes* started in a dead branch stub by winged reproductives and *Co. acinaciformis* foraging from their mound-nest into the trunk via the roots.

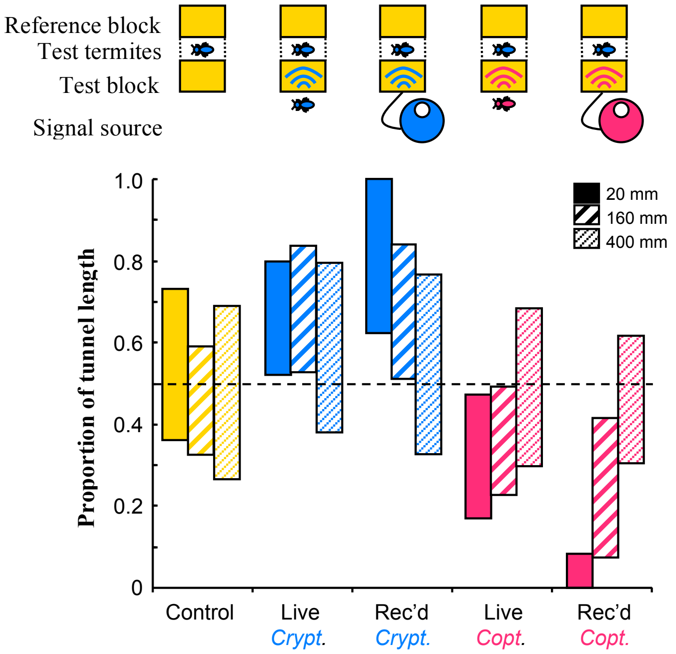

Figure 2: 95% confidence intervals of the proportion of the total tunnel length excavated by test termites in the test block (receiving different signal treatments). Test termites were *Cryptotermes*; test blocks received a signal either from live termites or from foraging vibration signals.

We tested the hypothesis that *Cryptotermes* were able to detect vibrations produced from feeding by *Coptotermes* and to avoid them[32]. We used *Cr. secundus* as test termites, which were offered two choices of wood for food. One choice received no signal (the 'reference' block), whereas the other (the 'test' block) either received no signal (the control) or received vibration signals from live termites (either *Cr. secundus* or the competitively dominant subterranean termite *Co. acinaciformis*) or feeding vibration signals recorded from these termites, as shown in Figure 2. There were 15 test *Cr. secundus* worker termites in each replicate. For signals from live termites, there were either 15 *Cr. secundus* workers or 300 *Co. acinaciformis* workers. The different termite numbers were a consequence of availability and physiology. A large number of *Co. acinaciformis* was necessary because they die rapidly in small groups isolated from their colonies under these conditions. It was found that for *Co. acinaciformis*, 300 was the smallest group size with any survivors at the end of the experiment. *Cr. secundus* colony size is usually less than 300 and their survival is usually very high because their water requirement is very low, only what they metabolize from their food. The difference in numbers of signal *Cr. secundus* and signal *Co. acinaciformis* is unlikely to cause a difference in signal activity because the cut end of the wooden blocks on which the termites chewed could only accommodate around 20 termites. Also, the activity rates in the recorded vibration signals are approximately the same for *Cr. secundus* and *Co. acinaciformis*. The experiment was run for two weeks in a constant environment room with 29°C and 80% RH. The number of replicates was 12, 15, 10, 15 and 12 respectively for treatments: control, live *Cr. secundus*, recorded vibration signals of *Cr. secundus*, live *Co. acinaciformis* and recorded vibration signals of *Co. acinaciformis*.

Results are plotted in Figure 2 in terms of the 95% confidence intervals (CI) of the proportion of the total tunnel length excavated by the test *Cr. secundus* termites in the test block receiving different signal treatments. A preference is observed when the 95% CI does not overlap the 0.5 dashed line; attraction to the test block is indicated by the 95% CI being above 0.5 and avoidance when below. Figure 2 shows that (a) there was no significant preference in all control block pairs (ie blocks of the same size without signals) and all 400 mm blocks; (b) the test termites (*Cr. secundus*) preferred 20 and 160 mm test blocks with vibration signals, either live or recorded, from the same species (*Cr. secundus*); and (c) the test termites (*Cr. secundus*) avoided 20 and 160 mm test blocks with vibration signals, either live or recorded, from the subterranean species (*Co. acinaciformis*). These results indicate that the drywood termite *Cr. secundus* workers can discriminate their own species from subterranean termites using only vibration signals, hence supporting the hypothesis that *Cr. secundus* workers use vibrations to avoid competitors.

3. Termites use vibrations to eavesdrop on predatory ants

Even though termites have evolved sophisticated defence adaptations, from biting to sprung jaws, phragmatic or blocking heads to glues and toxins[35, 36], it is assumed that termites primarily rely on hiding or building clay structures to avoid ant predation[31, 37]. Clearly the termites were avoiding detection even though they were within a few millimetres of ants (Figure 3). Avoiding detection is the major defence of termites[38, 39], either by eating their food from the inside out[28, 40], or as we have discovered[31], by hiding behind their defences built from clay. Yet termites cannot hide continuously, as this would prevent exploration for and discovery of new food resources. Termites, therefore, would require predator detection. As we have shown[32], the drywood *Cr. secundus* worker termites communicate vibro-acoustically and they are able to eavesdrop to discriminate their own species from the subterranean species, *Co. acinaciformis*, hence avoiding their competitors. It seems possible that termites could also detect ants utilising this ability, and hence avoid them.

We conducted choice experiments by using the set-up in Figure 4 (showing only 1 cylindrical container and part of a rectangular box) to test whether termites detect ants using mechanical or chemical cues. Termites (10 g / 2040 individuals of *Co. acinaciformis*) were held inside the rectangular box with moist vermiculite and fresh *Pinus radiata* sawdust. Two *P. radiata* wooden discs (ca. 1 mm thick) separating the termites in the rectangular box from the two cylindrical plastic containers (one always empty and one for experimental treatments) were for the termites to eat. There were five different treatments for one container: ‘empty’ = nothing in cylinder; ‘live ant’ = 12 live *Iridomyrmex purpureus* (South Eastern ‘blue form’); ‘dead ant’ = 12 dead ants (killed by freezing at -10° C for 60 minutes), ‘recorded ant signal’ = playback of 12 ants recorded walking on a wooden disc; and ‘pink noise’ = playback of synthesized pink noise signal. We used five combinations of treatments in the choice experiment, as shown in Figure 5: Case A with 50 replicates, empty + empty (a double control); Case B with 57 replicates, empty + dead ants (chemical signal); Case C with 30 replicates, empty + live ants (both chemical and mechanical signals); case D with 17 replicates, empty + recorded ant signal (mechanical signal); and case E with 11 replicates, empty + pink noise (mechanical signal control). The playback of a recorded ant-walking signal is the control for the setup with live ants. The walking signals produced by twelve *Ir. purpureus* were recorded using a Polytec PDV-100 single point laser vibrometer (sampling at 12 kHz) in an apparatus with an air-cushioned passive vibration table (Kinetic Systems, Boston, MA ELpF) to isolate it from the support in a 28°C temperature-controlled anechoic chamber, as shown in Figure 6.

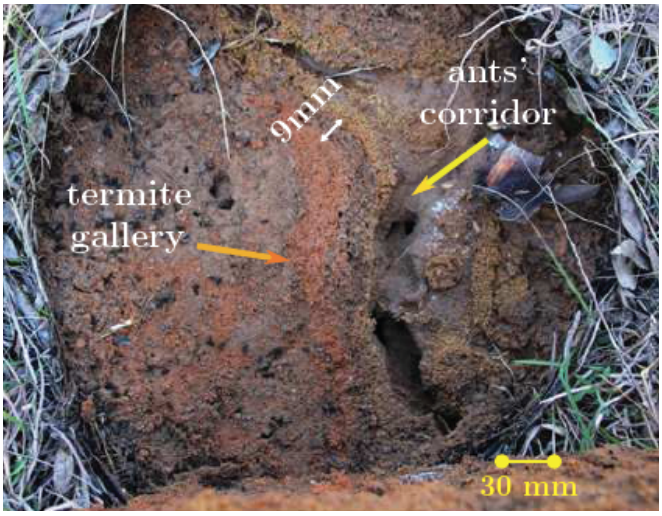

Figure 3: Proximity of termite and ant tunnels revealed in the soil covered by a wooden disc.

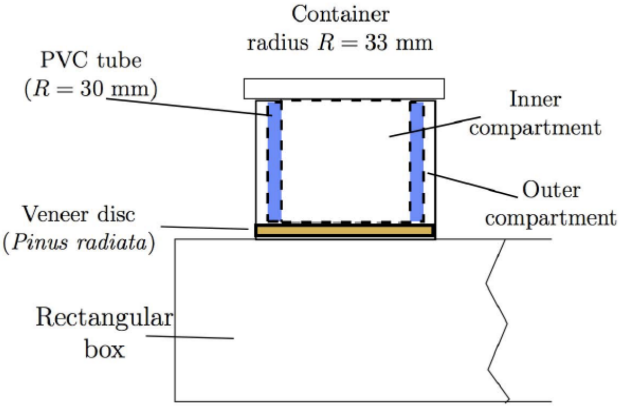

Figure 4: Schematic of experimental set-up showing the rectangular box housing *Co. acinaciformis* and one of two cylindrical containers.

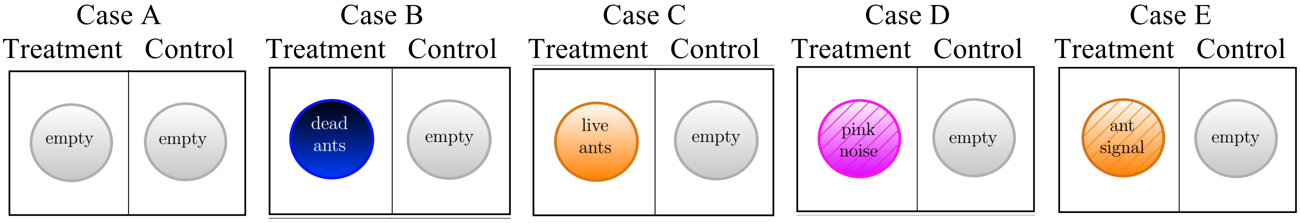

Figure 5: Schematic diagram showing various treatments for choice experiments.

We ran the experiments for 48 hours in an environmental chamber (28°C, 80% RH, 5 × 3 m, 65 dB(A) background noise level). The recorded signals were played back using a Sony Diskman (Tokyo) connected to a shaker (Philip Harris, Leicestershire, UK) as an excitation source, which was glued to the wooden discs. The shaker was hung on a polyester shock cord (100% elongation at 1.477 kg load), and the insect boxes were positioned on foam to minimise transmission of extraneous signals. At the end of the experiment, we dry weighed the wooden discs to obtain an estimate of the consumed wood. We normalised data with respect to the sum of wood removed per container and we conducted median tests using boxplots. The raw data was further analysed using box-cox transformation and two sample one-way ANOVA tests (equivalent to paired *t*-tests)[41].

Results show that the termites ate through the wooden disc in two patterns revealing that they were making use of information contained in mechanical cues. In the first pattern, termites chewed through both wooden discs for case A: empty + empty (double control, $n=50$, $df=101$, $F=0.4$, $p=0.53$); case B: empty + dead ants ($n=57$, $df=113$, $F=0.07$, $p=0.79$); and case D: empty + pink noise ($n=11$, $df=21$, $F=0.39$, $p=0.54$). In the second pattern, the termites chewed through the empty (control) wooden disc only for case C: with empty + live ants ($n=30$, $df=59$, $F=8.56$, $p<0.01$); and case E: the empty + recorded ant signal ($n=17$, $df=33$, $F=8.03$, $p<0.01$). The results in Figure 7, expressed as normalised wood eaten per hour in box plots, clearly show that although the 99% confidence intervals overlap in Case A, Case B and Case D, they do not overlap in Case C and Case E;

thus the difference in the medians of treatment and control for both Case C and Case E is significantly different at p<0.01, indicating that the termites avoided ants based on vibration cues.

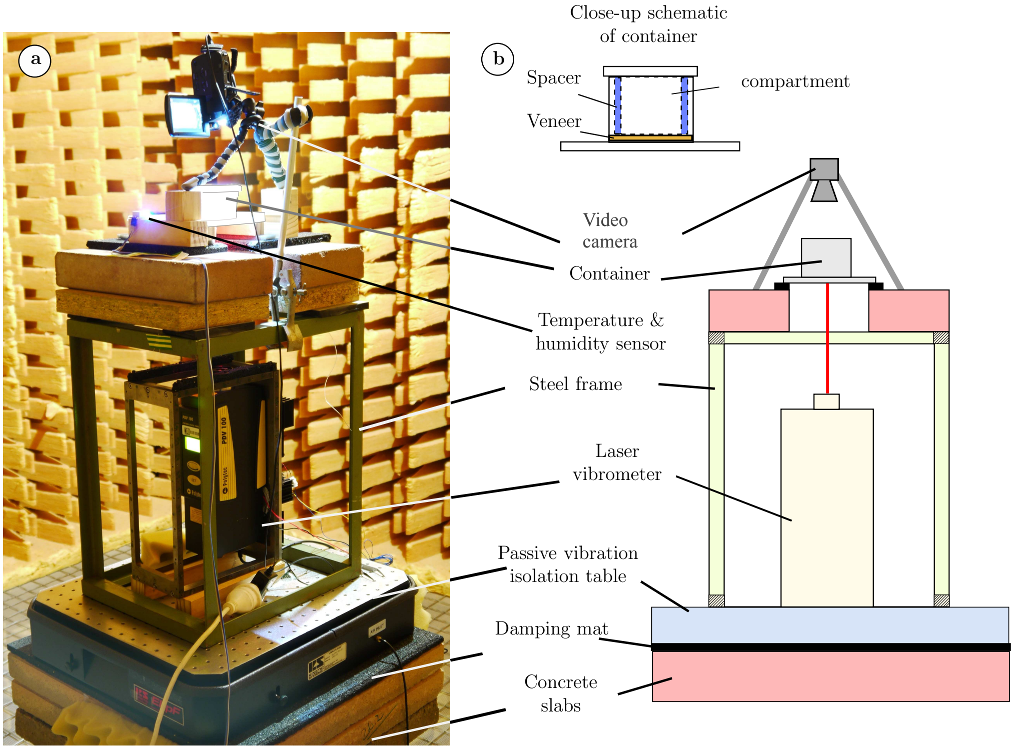

Figure 6: Apparatus for recording ants walking signals in an anechoic chamber.

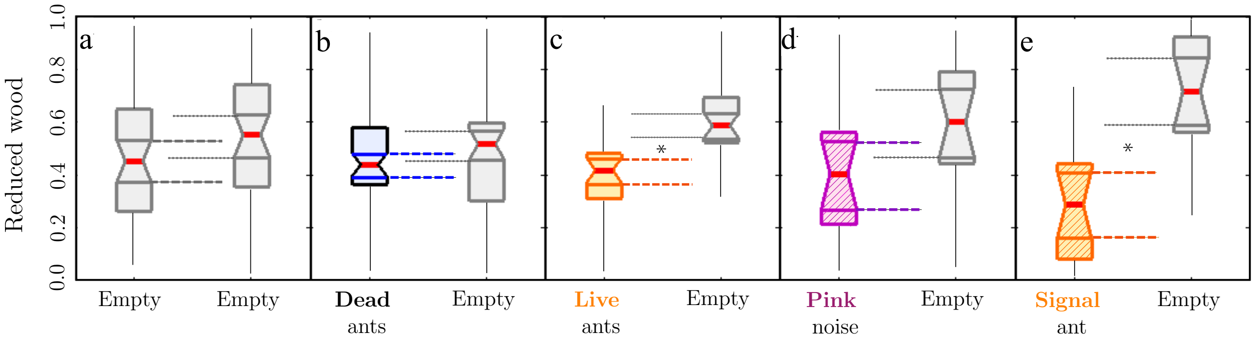

Figure 7: Wood eaten by termites from the wooden floors of the cylindrical containers, shown as box plots of proportion of wood weight reduction per hour: medians are red central lines, notches are 99% confidence intervals, boxes are 25 and 75 percentiles, and whiskers are the minimum and maximum values. The experimental pairings were: (a) control only (two empty chambers); (b) chemical signal (dead ants); (c) chemical plus vibration signal (live ants); (d) control vibration signal (pink noise); (e) vibration signal (playback of recorded ants).

4. Conclusions

Our research in the last decade was the first to show that termites use vibrations to determine the quantity and quality of food. While food is an important consideration in making foraging decisions, termites have often been found to forage in the vicinity of competitors and/or predators without being discovered. For example, the drywood termites *Cryptotermes* and subterranean termites

C*optotermes* are often found co-existing in the same tree, while the subterranean termites are often found foraging only millimetres away from predatory ants. Here, we review our most recent research to show that (a) the drywood termite workers *Cr. secundus* use vibration produced from feeding by their competitors, *Co. acinaciformis* to eavesdrop on them and hence avoid them; and (b) the subterranean termite workers, *Co. acinaciformis*, use vibrations produced on the substrate from walking by their predatory ants, *Ir. purpereus*, to eavesdrop on them and hence avoid them. Considering that 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, their abilities to use vibrations to thrive in a predators' world are remarkable feats. How termites process vibration signals from various sources in the presence of normally high environmental vibrations and noise to make foraging decisions is still not known. The discovery of this mechanism is yet to be made and will present an exciting challenge for the community of researchers in vibrations, acoustics, signal processing and biology to collaborate.

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