Termites eavesdrop to avoid competitors

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1. INTRODUCTION

Competition exclusion, when a single species dominates resources due to superior competitiveness, is seldom observed in nature. Termites compete for resources with deadly consequences, yet more than one species can be found feeding in the same wooden resource. This is especially surprising when drywood species, with colonies of a few hundred, are found cohabiting with subterranean species, with colonies of millions. Termites communicate vibro-acoustically and, as these signals can travel over long distances, they are vulnerable to eavesdropping. We investigated whether drywood termites could eavesdrop on vibration cues from subterranean species. We show, using choice experiments and recordings, that the drywood termite Cryptotermes secundus can distinguish its own species from the dominant competitor in the environment, the subterranean termite Coptotermes acinaciformis. The drywood termite was attracted to its own vibration cues, but was repelled by those of the subterranean species. This response increased with decreasing wood size, corresponding with both increased risk and strength of the cue. The drywood termites appear to avoid confrontation by eavesdropping on the subterranean termites; these results provide further evidence that vibro-acoustic cues are important for termite sensory perception and communication.

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Korb & Katrantzis 2004; Korb & Schmidinger 2004). Cryptotermes colonies contain few (sometimes only one) defensive soldiers, which have relatively small jaws, instead relying on their phragmatic heads to block tunnels. Also, drywood termite colonies remain within the single tree or piece of wood as they are unable to tunnel through soil, thus preventing escape.

In comparison, Coptotermes are strong competitors. They are the dominant wood-eating termite in Australia; they infest more than 85 per cent of trees (Hill 1942; Werner et al. 2008). 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 thousands of aggressive soldiers with long biting mandibles and sticky glue secretions (Evans et al. 1998, 1999). 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 (Hill 1942; Greaves 1959)—and so produce the raw material for the Aboriginal musical instrument, the didgeridoo (Tarnopolsky et al. 2005; Werner et al. 2008; figure 1). Despite the apparently overwhelming competitiveness of Coptotermes, Cryptotermes colonies can coexist in Coptotermes-infested trees (Hill 1942; Gay & Watson 1982).

We tested the hypothesis that Cryptotermes were detecting Coptotermes and avoiding them. Termites generate vibrations when they chew and they use these vibrations to determine wood size and the quality of the food source (Evans et al. 2005, 2007; Inta et al. 2007). Given that termites use vibration alarm signals generated by soldiers (Howse 1964; Röhrig et al. 1999; Inta et al. 2009), it seemed possible that species could detect other species using just vibration signals or cues from vibrations caused during feeding.

2. MATERIAL AND METHODS

(a) Test species
We used the co-existing termite species Cryptotermes secundus and Coptotermes acinaciformis (Hill 1942; Gay & Watson 1982), and collected the Cr. secundus from trees and the Co. acinaciformis from mound nests in the field near Darwin, Northern Territory, Australia (latitude 12.4°S, longitude 130.9°E). We housed the termites in constant-temperature rooms (28°C and 80% RH) in Canberra. We used 5070 Cr. secundus ‘workers’ from 31 colonies (4290 as test termites and 780 as cue termites) and approximately 16 800 Co. acinaciformis workers from five colonies as cue termites. Although often referred to as workers, the drywood termites that help in the colony are not true workers, but totipotent nymphs that have delayed development (see Korb & Katrantzis 2004; Korb & Schmidinger 2004).

(b) Laboratory bioassays
We had three sizes of paired wooden blocks: 20, 160 and 400 mm long. We used these different block sizes to test the hypothesis that Cr. secundus detect and avoid Co. acinaciformis only when the perceived risk was high, with risk inversely correlated with distance to Co. acinaciformis. To ensure paired blocks would be as similar as possible, we cut them sequentially from lengths of seasoned, air-dried Pinus radiata wood of 20 × 20 mm cross section. The ‘test termites’ were those whose behaviour was under test. There were 15 test Cr. secundus termites in each replicate, which were held in a 15 mm long central chamber made from tape, aluminium foil and/or plastic sheeting between the just-cut surfaces of the paired blocks; thus, the test termites encountered two almost identical wooden faces.

The ‘cue termites’ were those that provided the cue, to which the test termites were exposed. We had four cue treatments: live Cr. secundus, recorded vibration cues of Cr. secundus, live Co. acinaciformis and recorded vibration cues of Co. acinaciformis. We also had a no-cue control. The cue treatment was applied to one wooden block in each pair. For the live termite cue treatments, we made cages from acrylic tube (20 mm diameter), aluminium foil and tape. A side chamber was placed on each free end (distal to the central chamber containing the test termites) of the paired wooden blocks; only one side chamber received termites, either 15 Cr. secundus workers or 300 Co. acinaciformis workers. Both side chambers in the Co. acinaciformis treatment had damp vermiculite clay to provide water (figure 2). 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; 300 was the smallest group size with any survivors at the end of the experiment, although there were often no survivors even for this group size. Cryptotermes secundus colony size is usually less than 300, so it was almost impossible to obtain numbers equal to those of Co. acinaciformis. However,
survival is usually very high, perhaps due in part to their water requirements; they need only what they metabolize from their food. The numerical difference was unlikely to equate to a difference in vibration cue activity as the cut end of the wooden blocks (on which the termites were able to chew) could accommodate only around 20 termites. More importantly, the activity rates in the recorded cues were equal for all species and wood block size combinations (see §2c), thus providing a control for signal termite numbers.

We played the recorded cues as .wav files from CDs (Sony D-EJ100) through Philip Harris vibration generators (model F4H31134, Leicester, UK), which were attached to the free end (distal to the central cell) of one of the paired wooden blocks using an aluminium beam and a wood screw. The CDs played continuously (24 h d$^{-1}$) for the duration of the experiment. The amplitude of the playback of the recorded cues was close to that of the cue termites, as measured by an accelerometer. We expected that the amplitude of the cue would give information primarily about distance of the receiving termite from the cue source, because of the attenuation of the signal amplitude of vibrations due to damping in the substrate. The acceleration frequency response of the vibration generator was relatively flat over the frequency range of interest (100 Hz to 10 kHz). The materials of the central chamber transmitted a negligible signal from the signal block side (more than 30 dB reduction in the acceleration from the block receiving the signal to the other block).

We ran the experiment for two weeks in a constant-environment room (29°C and 80% RH). Tunnelling data were analysed using SYSTAT 9 (SPSS). We used only replicates with surviving termites in the analysis; these included for each treatment (20, 160 and 400 mm blocks, respectively): live Cr. secundus (15, 20, 17), recorded vibration cues of Cr. secundus (10, 24, 18), live Co. acinaciformis (15, 23, 20), recorded vibration cues of Co. acinaciformis (12, 21, 30) and no-cue control (12, 34, 17). Two-way and one-way ANOVA with Bonferroni-corrected post hoc comparisons were used to compare distance and proportion distance tunnelled. We determined preference by calculating 95 per cent confidence intervals of proportion distance tunnelled in the block receiving the cue; we considered those not overlapping 0.5 to have made a choice.

(c) Recorded cues

The recorded cue treatments were designed to control for any confounding effect of species and number of individual cue termites used in the live termite treatments. We recorded termites from six Cr. secundus colonies, and three Co. acinaciformis colonies feeding on wooden blocks of Pinus radiata of 20, 160 and 400 mm length under identical conditions in an anechoic chamber to minimize environmental noise and reflected cues. The termites were held in the wooden blocks for 1–5 days, and we recorded cues throughout this time. We used a Bruel & Kjaer 4370 accelerometer attached to the opposite end of the wooden blocks to the termites and a Bruel & Kjaer 2635 charge amplifier, and recorded the cues directly to the hard drive of a computer using a soundcard.

We assembled six composite recorded cues, each 10 min in duration, one for each species–block size combination. The recorded cues were composite because they were made from shorter recordings from several groups from each of the colonies for each species. We did this to prevent confounding species identity and individual colony identity and also to ensure the same level of activity in each recorded cue for each species–block size combination. There were two obvious types of activity in the cues: (i) long, dull-sounding ‘scratches’ made when the termites dragged their mandibles across the wooden surface and (ii) short, sharp ‘snaps’ made when wooden fibres broke. The recorded Cr. secundus cues had 71.1 ± 1.8 scratches min$^{-1}$ (mean ± s.e.) and 8.8 ± 1.0 snaps min$^{-1}$, and the recorded Co. acinaciformis cues had 70.7 ± 1.7 scratches min$^{-1}$ and 9.2 ± 0.5 snaps min$^{-1}$. The quantity of each activity (log transformed to meet homogeneity of variance assumptions) of the composite recorded cues were not significantly different when compared with a two-factor ANOVA with species and block size as treatments: scratches (species $F_{1,54} = 0.018$, $p = 0.894$; block size $F_{2,54} = 0.259$, $p = 0.773$, interaction $F_{2,54} = 0.050$, $p = 0.951$); snaps (species $F_{1,54} = 1.658$, $p = 0.203$; block size $F_{2,54} = 1.044$, $p = 0.359$, interaction $F_{2,54} = 0.013$, $p = 0.987$).

3. RESULTS

Test Cr. secundus termites tunnelled a similar total distance (i.e. tunnel length in both paired blocks added) between cue treatments (approx. 12 mm), but tunnelled significantly further in the longest blocks (approx. 10 mm versus 13 mm; cue treatment $F_{4,275} = 0.188$, $p = 0.944$; length treatment $F_{2,275} = 6.621$, $p = 0.002$; figure 3). This result showed that the termites contributed the same feeding effort between cue treatments, but more effort when more food was available, in agreement with previous results (Lenz 1994; Evans & Gleeson 2006).

To control for the effect of wood block size, we converted data to proportion of tunnelling in the block receiving the cue for the live termite and recorded cue treatments, or in a random block for the controls. There was a significant interaction ($F_{4,271} = 2.066$, $p = 0.039$) between cue type and block length; therefore, each block size was analysed separately. For 20 mm long
wooden blocks, cue treatments were significantly different ($F_{4,59} = 14.755$, $p < 0.001$), with live *C. secundus* not significantly different from recorded *C. secundus* ($p > 0.05$) and live *C. acinaciformis* not significantly different from recorded *C. acinaciformis* ($p > 0.05$), but with both *C. secundus* treatments significantly different from both *C. acinaciformis* treatments ($p < 0.05$; all post hoc comparisons Bonferroni corrected). The same situation was observed for 160 mm long wooden blocks: treatments were significantly different ($F_{4,115} = 5.590$, $p < 0.001$), with live *C. secundus* not significantly different from recorded *C. secundus* ($p > 0.05$) and live *C. acinaciformis* not significantly different from recorded *C. acinaciformis* ($p > 0.05$), but with both *C. secundus* treatments significantly different from both *C. acinaciformis* treatments ($p < 0.05$; all post hoc comparisons Bonferroni corrected).

The situation differed for 400 mm long wooden blocks: no treatments were significantly different ($F_{1,97} = 0.283$, $p = 0.889$; figure 4).

The preference of the test *C. secundus* was confirmed by calculating 95 per cent confidence intervals on the proportion of tunnelling in blocks receiving the cue. When the 95 per cent confidence intervals did not overlap 0.5, the test termites were determined to have a preference. *Cryptotermes secundus* preferred 20 and 160 mm blocks with live *C. secundus* and recorded *C. secundus* cues; they avoided 20 mm and 160 mm blocks with live *C. acinaciformis* and recorded *C. acinaciformis* cues (figure 5). Test *C. secundus* had no preference in all control block pairs and all 400 mm blocks.

### 4. DISCUSSION

These results show clearly that termites were using vibration cues to distinguish their own species from others, at least at shorter distances. It was unlikely that the test *C. secundus* could have detected the cue termites by other means, e.g. chemically, because they were completely contained and distant from the test termites.

However, this possibility could not be ruled out; yet the recorded cues of both species produced the same pattern as the live termites, thus confirming that the test *C. secundus* termites were responding to the vibration cues alone. The recorded cues produced a greater response than the live termites, perhaps because the vibration cues were played continuously, whereas live termites may have chewed on the wooden blocks less constantly. There are two lines of support for this suggestion. First, the recorded cues were composite, with shorter recordings of higher activity cut from longer recordings, and so were likely to have higher activity overall than the live cue termites. Second, the related species *Coptotermes lacteus* varied the numbers of foraging termites found in feeding stations over the 24 h day (Evans & Gleeson 2001), indicating that the vibration cues generated by chewing varied with foraging activity over the day.
The ability to detect vibrations made by feeding and perceive the species feeding could be considered a form of eavesdropping. This is distinct from eavesdropping in the usual sense of the term, when one prey species listen to the alarm calls of other prey species to detect the presence of predators (Seyfarth & Cheney 1990; Otter et al. 1999; Zuberbühler 2000; Templeton & Greene 2007), but it is analogous to the eavesdropping on foraging signals of competitors observed in bees. The sweat bee Halictus aerarius avoids flowers visited and marked by other conspecifics and heterospecific bee species. This increases their foraging efficiency as H. aerarius can avoid flowers emptied of nectar (Yokoi et al. 2007). Similarly, bumblebees and honeybees avoid the flowers visited by hoverflies (Reader et al. 2005). Perhaps the closest analogous behaviour is that of Melipona rufiventris, a stingless bee. This bee can detect and avoid the odour marking of a competitor stingless bee, Trigona spinipes, because T. spinipes attacks and usurps the food resources of M. rufiventris (Niek et al. 2004).

Thus, two ecologically subordinate species, the stingless bee M. rufiventris and the drywood termite Cr. secundus, can eavesdrop on and avoid their ecological dominants.

The ability to identify other termite species from vibration cues or other signals has not been identified before now. Vibration cues have several advantages: they are fast, operate over distance and do not require direct contact—a particularly useful advantage for cryptic animals—although operation over distance allows eavesdropping. The decrease in response with the increase in wooden block size may suggest that the termites are capable of evaluating risk (i.e. by avoiding competitors only when the threat is imminent). Alternatively, it is possible that the termites’ ability to perceive the cue diminishes as the block size increases. The benefit in avoiding Co. acinaciformis was clear, even more so when they were close (in fact, the Co. acinaciformis tunnelled through the 20 mm block in two replicates and killed all the test Cr. secundus; these were not used in the analysis). However, the benefit in having attraction to conspecifics is less clear. One possibility may be the opportunity for outbreeding. Should Cr. secundus colonies be orphaned (i.e. the mother queen or father king, or both, die), the workers can mature into neotenic replacement reproductives. Without meeting another colony, newly reproductive brothers and sisters will be forced to mate. This seems plausible as Cr. secundus colonies accept unrelated individuals peacefully and genetic data suggests that around 25 per cent of field Cr. secundus colonies are from two or more colonies merging (Korb & Schneider 2007).

Perhaps it is not surprising that termites are using vibration cues and signals, because they are small, herbivorous insects, which, due to their size and physiological constraints, are well adapted to use substrate-borne vibration signals (Bennet-Clark 1998; Cocroft & Rodriguez 2005). It is not clear whether subterranean termites have this ability. Perhaps they do, but they have lower selective pressure to avoid competitors, due to their greater competitive ability and foraging in more than one wooden resource. Evidence to support this suggestion could come from similar experimental studies comparing species of subterranean termites that are relatively stronger and weaker competitors. Alternatively, it is possible that subterranean termites may be less attuned to vibration cues and signals than drywood termites because of the medium in which they live and nest. Soil has a much larger coefficient of attenuation than wood (Liu & Nagel 1993), so the detection range of acoustic emissions in soil can be low, as little as 5 cm (Mankin et al. 2000). If so, then drywood termites can exploit the same food resources as subterranean termites by being even more cryptic than subterranean species. While it has been shown here that drywood termites distinguish their own species from others using vibration cues through wood, exactly which features of these cues and signals the termites use to extract the information and how they process such information are yet to be determined; such information has yet to be determined even for birds (Templeton & Greene 2007; Magrath et al. 2009). More detailed study on the features of the vibration cues is required, as well as comparative studies with other subterranean species to determine how widespread this ability is in the Isoptera.

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