

RESEARCH ARTICLE

Vibrational long-distance communication in the termites *Macrotermes natalensis* and *Odontotermes* sp.

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SUMMARY

Fungus-growing higher termites build long subterranean galleries that lead outwards from the nest to foraging sites. When soldiers are disturbed, they tend to drum with their heads against the substrate and thereby create vibrational alarm signals. The present study aimed at describing these acoustic signals, how they are elicited, produced and perceived, and how these signals propagate within the galleries and nests over long distances in two termite species of the Southern African savannah, *Macrotermes natalensis* and an *Odontotermes* sp. The signals consist of trains of pulses with a pulse repetition rate of 10–20 Hz. The galleries have physical features that promote vibrational communication and are used as channels for long-distance communication. In *M. natalensis*, the signal propagation velocity is $\sim 130 \text{ ms}^{-1}$ and the signals are attenuated by $\sim 0.4 \text{ dB}$ per centimetre distance. Nestmates are extremely sensitive to these vibrations with a behavioural threshold amplitude of 0.012 ms^{-2} . Workers respond by a fast retreat into the nest and soldiers are recruited to the source of vibration. Soldiers also start to drum with a reaction time of about 0.3 s, thereby amplifying the intensity of the signal. This social long-distance communication through chains of signal-re-amplifying termites results in a relatively slow propagation (1.3 ms^{-1}) of the signal without decrement over distances of several metres.

Key words: Isoptera, vibrational communication, signal transmission, alarm communication.

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INTRODUCTION

Termites are among the most important animals in tropical ecosystems. In the African savannah the turnover of organic matter by termites is roughly comparable to that of mammalian herbivores (Bignell and Eggleton, 2000). Their ecological success is based on their social organisation. The pronounced differentiation of several castes along with division of labour facilitates the construction of huge mounds several metres in height in which some species grow fungi. Both the mechanical protection provided by the mound and provisioning the colony by continuously growing suitable food for the colony members make the termites more independent from environmental factors. Such tasks are only manageable with a sophisticated intracolony communication system. In contrast to solitary insects, which communicate mainly with potential mates or potential competitors, there is a variety of other contexts in which social insects and especially termites communicate. For example, many species have evolved systems of alarm communication or recruit nestmates to exploit resources fast and efficiently (Greenfield, 2002; Kirchner, 1997). Many studies document the importance of chemical communication in termites (Bordereau and Pasteels, 2011). Pheromones coordinate different social interactions, including foraging, building, mating and defence (Costa-Leonardo and Haifig, 2010), whereas little is known about acoustic communication. Spiders have been used as model systems to study substrate-borne vibratory communication (Hergenröder and Barth, 1983), in particular wolf spiders of the genus *Schizocosa* (Elias et al., 2006; Elias et al., 2010; Gibson and Uetz, 2008). Vibratory communication is far more prevalent in insects than communication through airborne sounds (Cocroft and De Luca, 2006). Substrate vibrations

are considered to provide a ubiquitous communication channel that is used alone or in combination with other information channels in multimodal signalling (Hill, 2009). Vibrational signals are used in the context of mate location and identification, courtship and mating, maternal care, foraging, predation and predator avoidance (Hill, 2009). For instance, vibrational antipredator signalling has been documented in several species of treehoppers. The aggregated offspring of *Umboia crassicornis* produce synchronous, vibrational signals that elicit defensive behaviours from their mother (Cocroft, 1996). Communication through substrate-borne vibrations has also been described in social insects like ants, bees and termites. Foraging workers of the leaf-cutting ant *Atta cephalotes* stridulate while cutting a leaf fragment. Workers respond to the vibrations transmitted through the plant material by orientating toward the source of vibration (Roces et al., 1993). Workers also stridulate when they are prevented from moving freely, for instance when a worker is buried by a cave-in of the nest. A stridulating ant attracts other workers, and if the ‘calling’ ant is covered by earth, intensive digging behaviour is released in the attracted nestmates (Markl, 1965).

Almost all investigations on vibrational communication in termites have been made in so-called lower termites. The lower drywood termites *Cryptotermes secundus* (Evans et al., 2007) and *Cryptotermes domesticus* (Evans et al., 2005) determine the size of a wood block (i.e. a piece of food) by using vibrations generated during foraging. The vibratory sense organ of termites is the subgenual organ, a chordotonal organ in the tibiae of the legs (Howse, 1964). Lower termites of the genus *Zootermopsis* live and feed in a single piece of wood (Weesner, 1970). Therefore, they do not have to forage outside their nests. When these termites are

disturbed, they tend to drum with their heads against the substrate and create a pulsed vibration. These drumming signals are trains of pulses of substrate vibrations with a pulse repetition rate of about 20 Hz (Kirchner et al., 1994; Stuart, 1988). Vibrations produced through head banging can be perceived by nestmates. Workers react with alarm and flee. Lower termites like *Zootermopsis* show no signal enhancement – they do not respond to drumming nestmates by drumming themselves. They display drumming behaviour merely as a response to disturbance of the nest. Therefore, signals are only transmitted over a short distance (Kirchner et al., 1994; Stuart, 1988).

Higher termites in the genus *Macrotermes*, best known for their enormous mounds in the African savannah, are fungus growers. To supply the fungus with dead dry plant material, they occupy a large territory around their nest. They build long subterranean galleries that lead outwards from the nest to their foraging sites. These gallery systems can spread over an area of up to 2000 m². The galleries are constructed underground; mounds consist of thick, massive walls (Jmhasly and Leuthold, 1999; Lys and Leuthold, 1991). This impressive architectural structure is probably the most promising way to avoid predation. Nevertheless, specialised predators, like aardvarks and pangolins with their powerful front legs, can open nests and galleries. The holes that these predators make in the nest are associated with air currents within the nest of which the termites are very aware (Connétable et al., 1999; Röhrig et al., 1999; Hertel et al., 2011). Also, a variety of invertebrate predators are of potential danger to foraging *Macrotermes*, particularly when the nest is damaged (Longhurst and Howse, 1979; Skutelsky, 1995). Ants are the most significant predators of termites and several species are more or less specialised on termite prey (Buczkoski and Bennett, 2007; Esquivel et al., 2004; Hölldobler and Wilson, 1990; Weber, 1964). Defending an extended nest system requires a communication system to inform nestmates in remote parts of the gallery about attacks and holes in the nest wall. The use of vibrational alarm signals that can be rapidly transmitted over long distances would allow fast retreat and defence reactions and would clearly be advantageous (Röhrig et al., 1999). Vibrational communication in higher termites has until now exclusively been studied in tropical species of *Macrotermes* (Röhrig et al., 1999) and *Pseudacanthotermes* (Connétable et al., 1999) in West Africa. The present study is focused on two species of the Southern African savannah and asks whether these species also use vibrational communication and, if so, how these signals are transmitted over long distances.

MATERIALS AND METHODS

Termites

Vibrational alarm communication was studied in the South African termites *Macrotermes natalensis* (Haviland) and an *Odontotermes* sp. The study was carried out between September 2009 and July 2011 at the Lajuma research centre in the western part of the Soutpansberg Mountain range, Limpopo Province, South Africa (23°22'1"S, 29°26'50"E). Species were identified following Uys (Uys, 2002). Their identification was confirmed by Uys. *Macrotermes* mounds were opened at their conical base to collect major soldiers for the laboratory experiments. Termites were maintained in plastic containers until used in experiments. Five *M. natalensis* colonies with a mound height between 1 and 1.5 m were used for the experiments. Experiments with *Odontotermes* sp. were made at their earth-covered above-ground foraging place.

Recording of substrate-borne drumming signals

Vibrational signals produced by termites were recorded on a two-channel digital audio recorder (M-Audio, Microtrack 2, Irwindale,

CA, USA) connected to a charge amplifier (Brüel and Kjaer 2635, Naerum, Denmark) and an accelerometer (B&K 4381). The accelerometer was mounted with wet nest material on the nest surface and in galleries leading from the nest to the foraging areas. Wet nest material dried within minutes, ensuring a very tight coupling.

Determination of threshold amplitudes of vibration in an artificial arena

To determine the termites' threshold amplitudes of vibration, artificial vibrations of a test arena were induced by a personal computer connected to an external sound card (Tascam US-144, Montebello, CA, USA) and a vibration exciter (B&K 4810) glued to the bottom of a Petri dish. The stimuli were sine waves of 1 s duration. To avoid artefacts at the beginning and end of the stimulus, the amplitude was increased and decreased with a ramp of 10 ms duration. The amplitude was increased in 6 dB steps until a behavioural reaction was observed. A major soldier was placed in a Petri dish (diameter 55 mm). To prevent termites from slipping, the Petri dish was coated with filter paper. The threshold amplitude of the soldiers' behavioural responses to vibrational stimuli was determined at different frequencies (100, 200, 500, 800, 1000 and 2000 Hz). The amplitudes of the stimuli were determined using a B&K 4381 accelerometer and a B&K 2635 charge amplifier. Stimuli were offered at 5 min intervals. For each frequency sequence, 10 new unstressed major soldiers were tested; stimuli and sham stimuli were presented in random order. The experiments were carried out blind – the observer was not aware of whether a stimulus or a sham stimulus was given. A response to a perceived stimulus was recorded when a termite changed its behaviour instantaneously (within 1 s): termites started or stopped moving, waved with their antenna or opened their mandibles. Chi-square analysis was used to test for deviation from expected values.

Propagation through the substrate – velocity and attenuation of drumming signals in the nest of *M. natalensis*

Artificial vibrations were induced by a personal computer connected to an external sound card (Tascam, US-144) and a vibration exciter (B&K 4810) mechanically coupled via a plastic stick (54 mm long, diameter 18 mm) to the galleries. Termite drumming was simulated by square-wave pulses with a pulse repetition rate of 11 Hz. Artificially produced drumming signals were recorded with a two-channel digital audio recorder (M-Audio, Microtrack 2) connected to two charge amplifiers (B&K 2635) and two accelerometers (B&K 4381). One accelerometer was placed 0.05 m distance from the vibration exciter. The second accelerometer was placed at various distances in this set-up. Both accelerometers were mounted at the bottom of the galleries in a horizontal orientation and were therefore mainly sensitive to vertical accelerations.

For measuring the propagation velocity of the primary wave (P-wave), the time delay of the first peak amplitude reaching the two accelerometers was compared as a function of the spatial distance between them. The propagation velocity of a slower wave was determined by cross-correlation of the spectrograms using the software Raven Pro 1.4 (Cornell Lab of Ornithology, Ithaca, NY, USA).

The attenuation properties of the substrate were calculated by comparing the peak amplitude levels at both measuring points. According to Born (Born, 1941), the amplitude of vibration waves decreases exponentially with distance: $A_x = A_0 e^{-\alpha x}$, where A_0 is the amplitude at a reference point, A_x is the amplitude at x cm distance from the reference point and α is the attenuation coefficient. By convention, the attenuation coefficient is given in dB cm⁻¹ (Aicher and Tautz, 1990): $\alpha_{10} = 10 \log_e \alpha$.

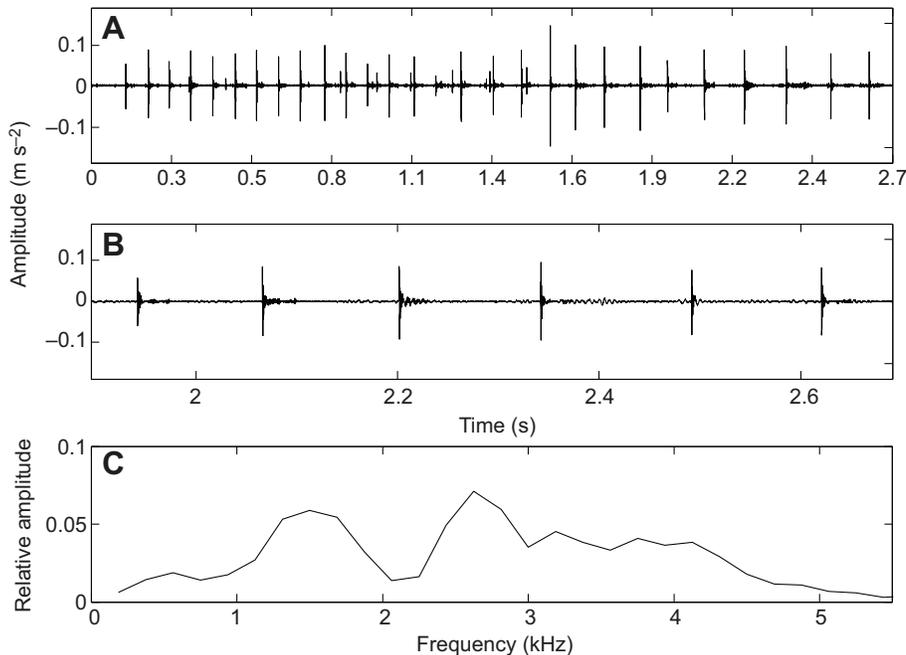


Fig. 1. Typical drumming signals of *Macrotermes natalensis*. (A) Oscillogram of several pulse groups produced by several termites. (B) Oscillogram of a pulse group produced by a single termite. The signal contains six pulses. The pulse repetition rate is 11 Hz. (C) Frequency spectrogram of the pulse group shown in B. Most energy is found between 1 and 5 kHz (band-pass filter 10 Hz to 10 kHz).

Context dependence of drumming signals – response to air puffs with different CO₂ levels

The response to air puffs with different CO₂ levels was observed in *M. natalensis* and *Odontotermes* sp. Three different air current stimuli (air from the surroundings, human breath and air from the surroundings enriched with 60% vol. CO₂) were used to investigate whether air currents can elicit drumming behaviour. Air stimuli were produced using a syringe, connected through a 1 m flexible tube to the nests. A total volume of 100 ml was delivered within about 0.7 s, resulting in an average flow rate of about 150 ml s⁻¹. The stimuli were tested in random order. Stimuli were given at 5 min intervals. The drumming response of the termites was recorded at a distance of 15 cm from the tube. The reaction time of termites was determined by measuring the time between the onset of a stimulus and the drumming response of the termites.

Kinematic and dynamic analysis of the drumbeat

A 1.5 m deep pit was dug close to a mound of *M. natalensis*. The central fungus chamber was opened from the side. This enabled video recordings of drumming termites from the side. High-speed video recordings were made with a Casio camera (Exilim EX-FH 20) at 1000 frames s⁻¹. The position of the labrum was marked in each frame. Two-dimensional video image analysis was used to calculate the velocity and attenuation of the drumbeat.

Transmission of drumming signals

The social transmission velocity of vibrational signals was measured in galleries of *M. natalensis* and *Odontotermes* sp. Two accelerometers were mounted at different distances within the galleries. Termite drumming was triggered with air puffs *via* a flexible tube mounted in the gallery close to one of the accelerometers. An air stimulus was produced using a 100 ml syringe with a flow rate of about 150 ml s⁻¹. The drumming response of the termites was recorded on two channels as reported before. We then measured the time delay between drumming signals produced in the vicinity of each accelerometer.

Recognition of pulse structure

To test whether vibrational signals are used in species recognition, artificial vibrations of different temporal structure were presented at the nests of *M. natalensis* and at the galleries of *Odontotermes* sp. We tested pulses with six different pulse repetition rates (8, 11, 14, 17, 20 and 23 Hz). Vibrational signals were generated by a personal computer connected to an external sound card (Tascam US-144) and a vibration exciter (B&K 4810) mechanically coupled to the nest/galleries. The sequence of stimuli was given randomly. Alarm drumming behaviour was taken as a response of the termites to the artificial vibrations. Termites alarm signals were recorded as described above.

RESULTS

Drumming signals

When disturbed, soldiers of *M. natalensis* hit the substratum with their heads, thereby producing a broadband vibrational signal that consists of a series of pulses. Each of the pulses arose from a single tap of the head against the ground. Typical drumming signals are shown in Fig. 1A. The number of pulses per signal varied between 5 and 22. The pulse repetition rate was 11 ± 3 Hz (mean ± s.d., *N* = 50; Fig. 1B). Most vibrational energy was found between 1 and 5 kHz (Fig. 1C).

The measured signal amplitudes were rather variable as a result of the different spatial distances of termites in relation to the recording accelerometer and the attenuation properties of the substrate. The highest recorded amplitudes were about 0.7 m s⁻².

Soldiers of *Odontotermes* sp. also drum with their heads against the substrate. Typical drumming signals are shown in Fig. 2A. The number of pulses per signal varied between 4 and 29. The pulse repetition rate was 19 ± 2 Hz (mean ± s.d., *N* = 50; Fig. 2B). The measured signal amplitudes were rather variable. The highest recorded amplitudes were about 0.4 m s⁻². Most vibrational energy was found between 2 and 3.5 kHz (Fig. 2C).

Vibration sensitivity in artificial arenas

Simulated substrate vibrations elicited responses in the entire range of tested frequencies (100–2000 Hz). Fig. 3 shows the threshold

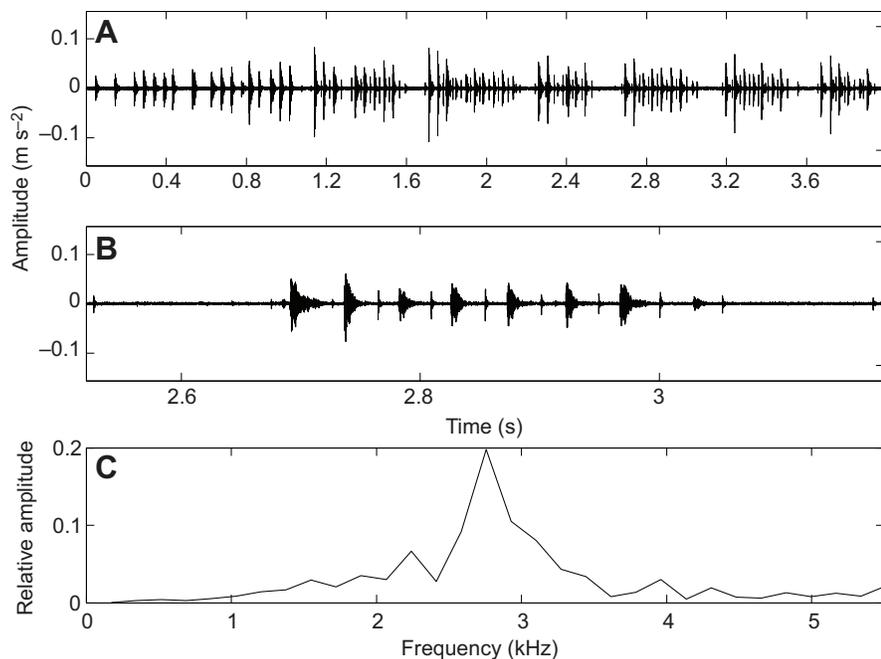


Fig. 2. Typical drumming signals of *Odontotermes* sp. (A) Oscillogram of several pulse groups produced by several termites. (B) Oscillogram of two pulse groups produced by two termites. The pulse repetition rate is 19 Hz. (C) Frequency spectrogram of the pulse group shown in B. Most energy is found between 2 and 3.5 kHz (band-pass filter 10 Hz to 10 kHz).

amplitude for *M. natalensis* tested in arena experiments. The termites are most sensitive to frequencies around 500 Hz. They are sensitive to amplitudes of about 12 mm s⁻² (range 9–19 mm s⁻²), which correspond to a displacement of the substratum of 1–2 nm.

Behavioural responses and reaction time to air stimuli

Drumming behaviour can be elicited by a flow of air in the gallery system of the nest. In *M. natalensis*, puffs of pure air elicited drumming responses in 44% of cases ($N=85$), human breath in 67% of cases ($N=57$) and CO₂ in 67% of cases ($N=73$). Human breath and CO₂ elicited a drumming response significantly more often than pure air ($P<0.01$, $\chi^2=11.52$, d.f.=2, Bonferroni correction, $N=215$). The median time delay between a disturbance and the initial drumming response of termites was 302 ms (range 9–923 ms, $N=92$).

In *Odontotermes* sp., puffs of pure air elicited drumming responses in 41% of cases ($N=22$), human breath in 57% of cases ($N=18$) and CO₂ in 100% of cases ($N=13$). CO₂ elicited a drumming response significantly more often than pure air and human breath ($P<0.01$, $\chi^2=8.19$, d.f.=2, Bonferroni correction, $N=53$). The median time delay between a disturbance and the initial drumming response of termites was 309 ms (range 211–702 ms, $N=25$).

Kinematic and dynamic analysis of the drumbeat

Major soldiers raised their head ~10 mm vertically in the air before accelerating it down to the ground. They hit the ground with the postmentum of their heads with a velocity of ~0.6 m s⁻¹ (median, $N=10$). Fig. 4A shows every fifth picture of a high-speed video. The position of the head is marked with a white dot. The first beat had the greatest velocity, reaching up to 1.5 m s⁻¹. The head was accelerated at ~107 m s⁻² (median, $N=10$). Fig. 4B shows the height of the soldier's head above the nest substrate while performing three beats.

Propagation velocity and attenuation of drumming signals in the nest of *M. natalensis*

The propagation velocity of the P-wave in the galleries was 171 m s⁻¹ (median, minimum 90 m s⁻¹, maximum 375 m s⁻¹, $N=107$). The slower wave propagated with a velocity of ~127 m s⁻¹ (median,

minimum 58 m s⁻¹, maximum 271 m s⁻¹, $N=17$). The attenuation properties of the galleries are shown in Fig. 5 as a function of the distance travelled in the substrate. The amplitude of the drumming signals propagated through the galleries was attenuated by 0.37 dB cm⁻¹ ($N=59$). The surrounding soil had similar attenuation properties, and drumming signals were attenuated by ~0.41 dB cm⁻¹ ($N=80$).

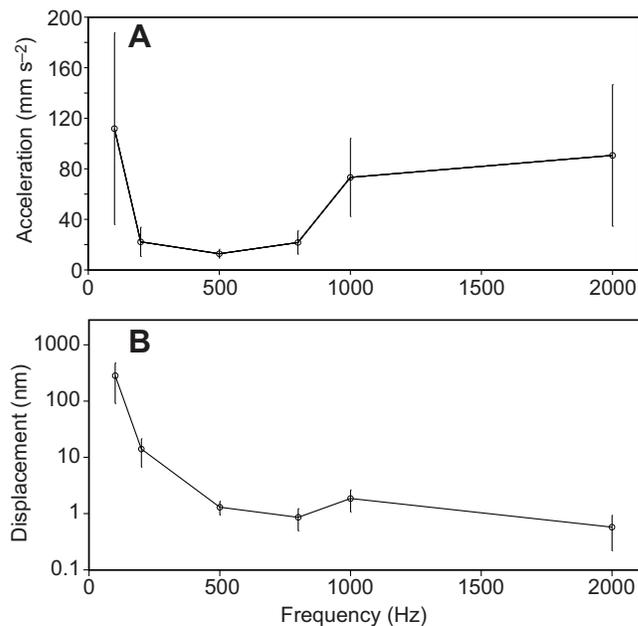


Fig. 3. Threshold amplitudes of vibrational stimuli eliciting a behavioural response in soldiers of *M. natalensis* (means \pm s.d.). The same data set is expressed as acceleration amplitude (A) and as displacement amplitude (B). The threshold amplitude of each termite is the lowest amplitude at which the response rate is significantly higher than the response rate to sham stimuli (χ^2 -test, $P<0.05$; $N=1200$ tests in total; $n=10$ termites for each frequency).

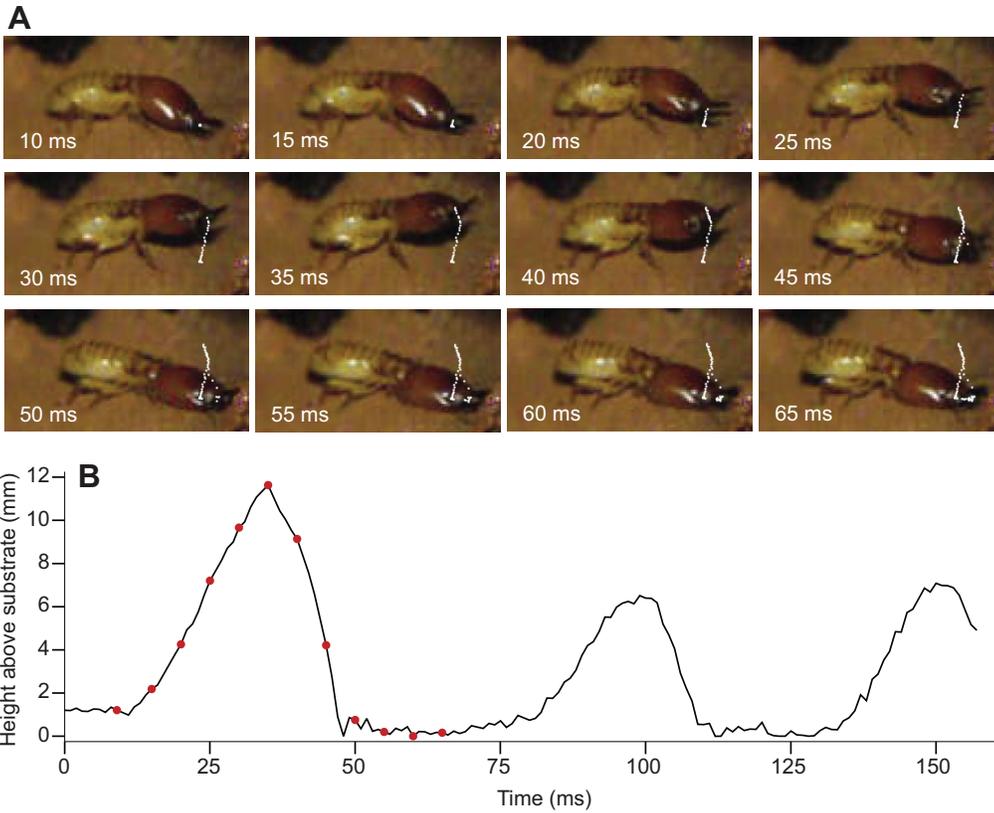


Fig. 4. (A) Single frames from a high-speed video recording (1000 frames s⁻¹) of a drumbeat of a major soldier of *M. natalensis*. Every fifth frame is shown. The position of the head is marked (white dot) in each frame. (B) Height of the termite's head above the nest substrate while performing three beats. The single frames shown in A are marked as red dots. Ten digitised traces like that in B were used for the kinematic analysis.

Long-distance alarm transmission

During the field experiments we often triggered alarm responses that spread over several metres. The velocity of this long-distance alarm propagation was 1.3 ms⁻¹ ($P < 0.01$, Pearson correlation, $R^2 = 0.549$, $N = 30$), much lower than the physical propagation velocity of substrate-borne vibration (Fig. 6). In *Odontotermes* sp., the velocity of long-distance alarm propagation was 2.1 ms⁻¹ ($P < 0.01$, Pearson correlation, $R^2 = 0.321$, $N = 13$; Fig. 7). Unlike the amplitude of signals produced by a single termite, which are propagated through the nest substrate and are strongly attenuated with distance, the vibration amplitude produced by chains of soldiers did not decrease at all.

Recognition of pulse structure

We could not find any indication that *M. natalensis* and *Odontotermes* sp. discriminate between vibrational stimuli with different temporal structure (Table 1). Neither *M. natalensis*

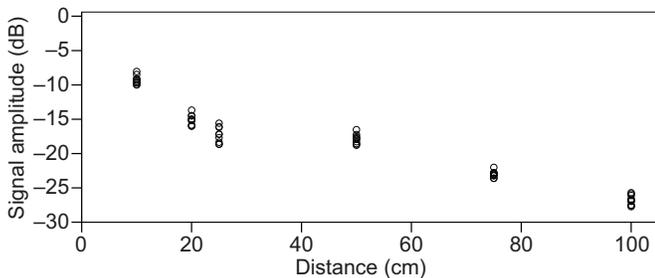


Fig. 5. Attenuation of the vibrational wave in the nest substrate of *M. natalensis*. The graph shows the difference in signal amplitude between accelerometers at various distances ranging from 10 to 100 cm ($N = 59$).

($P = 0.757$, $\chi^2 = 2.626$, d.f. = 5, $N = 112$) nor *Odontotermes* sp. ($P = 0.781$, $\chi^2 = 2.47$, d.f. = 5, $N = 128$) reacted significantly differently to vibrational stimuli with different pulse structures. In addition, the response rates to the tested vibrational stimuli were not significantly different between the two species (Table 1: χ^2 -test, d.f. = 1).

DISCUSSION

Here, we report for the first time vibratory alarm signals in higher termites of the Southern African savannah. Major soldiers of *M. natalensis* produced a vibratory alarm signal with a pulse repetition rate of about 11 Hz. The sympatric living termite *Odontotermes* sp. also produced drumming signals but with a pulse repetition rate of 19 Hz. Both termite species were able to transmit the alarm signals

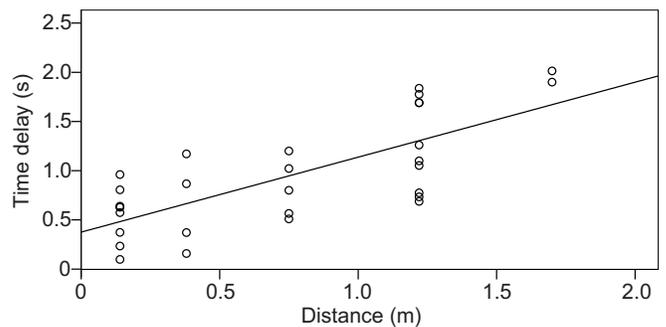


Fig. 6. Long-distance communication of *M. natalensis*. The time delay within chains of drumming termite soldiers is plotted as a function of spatial distance between the drummers. The velocity of alarm transmission is apparent from the linear regression gradient (Pearson correlation, $R^2 = 0.549$, $P < 0.01$, $N = 30$). The alarm transmission velocity is 1.3 ms⁻¹.

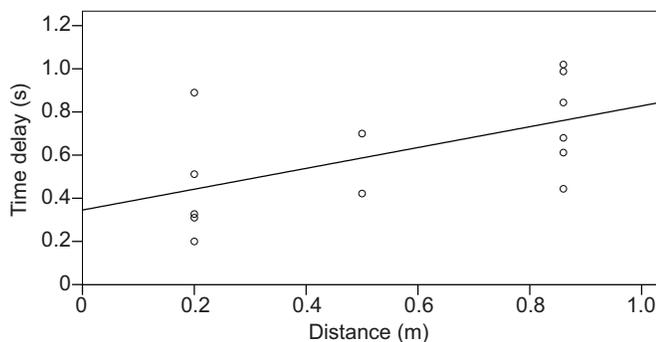


Fig. 7. Long-distance communication of *Odontotermes* sp. The time delay between drumming signals in chains of drumming termites is plotted against spatial distance between the drummers. The velocity of alarm transmission is apparent from the linear regression gradient (Pearson correlation, $R^2=0.321$, $P<0.01$, $N=13$). The alarm transmission velocity is 2.1 ms^{-1} .

over long distances. This ability is vital for termites that harvest in large groups and are frequently attacked by a variety of predators. Although long-distance alarm communication has been observed in Macrotermitinae before (Connétable et al., 1999; Röhrig et al., 1999), it was unclear exactly how the alarm was transmitted over long distances and whether subterranean galleries are used as communication channels.

Pheromones play a crucial role in the ecology of foraging in termites. During foraging, termites are exposed to a high predation risk. A variety of predators are more or less specialised on termites (Buczowski and Bennett, 2007; Kok and Hewitt, 1990; Redford, 1984; Wilson and Clark, 1977) and termites have evolved alarm pheromones (Šobotnik et al., 2008). However, previous studies have shown that in *Pseudacanthotermes spiniger*, *Pseudacanthotermes militaris* (Connétable et al., 1999), *Macrotermes subhyalinus* and *Macrotermes bellicosus* (Röhrig et al., 1999) neither tactile contacts nor pheromones are necessary to propagate the alarm. Similarly, trail pheromones are unlikely to play a dominant role in the fast alarm transmission in *Macrotermes*. Alerted soldiers do stay at the foraging site, probably in order to defend the nest. Workers flee from attacked foraging sites and may lay down pheromone trails while returning to the nest, but their walking speed is too slow to explain the transmission velocity of about 1.3 m s^{-1} of the spreading drumming alarm. Under conditions where a fast alarm transmission along the gallery is advantageous, vibrational signals are more efficient.

Our results confirm and extend the findings of a previous study of two *Macrotermes* species in West Africa (Röhrig et al., 1999). The mechanism of communication in *M. natalensis* is similar; our more detailed measurements, however, allow a deeper analysis of signal propagation and transmission. This alarm communication is composed of the physical propagation of the vibrational wave in

the substrate as well as the social amplification and transmission of the signal through positive feedback mechanisms. Both processes are characterised by specific and very different velocities of propagation and attenuation with distance.

The velocity of propagation of individual vibrational signals in the nest substrate was found to be about 130 ms^{-1} . This is in accordance with the results of previous biological studies (Aicher and Tautz, 1990; Brownell, 1977; Röhrig et al., 1999; Hanrahan and Kirchner, 1994). It should be noted that these propagation velocities are much lower than velocities calculated based on extrapolation from large-scale seismic data.

The attenuation of the signal with distance in the gallery system of the termites was not different from the attenuation in the surrounding soil. It was similar to attenuation found in comparable substrates (Aicher and Tautz, 1990; Röhrig et al., 1999; Hanrahan and Kirchner, 1994). The range of the signals, however, was dependent on the signal amplitude at the signal source, physical attenuation on the way to the receiver and the threshold of the receiver. The highest recorded amplitude in *M. natalensis* was 0.7 ms^{-2} . Based on a signal attenuation of 0.4 dB cm^{-1} and a threshold amplitude of 0.012 ms^{-2} , the range of this signal is about 0.4 m. This means that primary alarm signals can alert nestmates in the vicinity but would not reach nestmates in metre-long galleries. A similar alarm signalling system is found in several lower termite species (Howse, 1984; Kirchner et al., 1994; Stuart, 1988).

The fact that soldiers respond to drumming nestmates in the vicinity by drumming themselves leads to significant changes in both attenuation of the signal amplitude with distance and the velocity of propagation. The observed transmission velocity of 1.3 ms^{-1} is a hundred times less than the physical propagation velocity of the physical wave. Given that the distances from the nest to the foraging sites range from a few to some tens of metres, this velocity leads to colony responses within seconds. In addition, the velocity of propagation allows calculation of the distance between termites in chains of signal-transmitting soldiers. Based on a reaction time of about 0.3 s, the social transmission velocity of 1.3 ms^{-1} corresponds with a maximum distance of about 0.4 m between drumming termites. As it is difficult to observe termites in undisturbed galleries in the field, we cannot confirm this pattern by direct observations. However, the maximum distance calculated based on transmission velocity and reaction time corresponds perfectly with the maximum distance of individual communication calculated based on signal amplitudes, attenuation with distance and thresholds of perception.

Signal attenuation with distance is reduced to zero by the described mechanism of social reamplification. Such a signal transmission without decrement seems to be rare in animal communication, but not unique in *Macrotermes*. When a predator attacks an aggregation of *Umbonia crassicornis* nymphs, the first nymphs that perceive the predator produce a vibratory pulse. This elicits additional signals from siblings and signalling rapidly spreads across the group. In response to vibratory signals from her offspring,

Table 1. Probability of eliciting alarm behaviour in *Macrotermes natalensis* and *Odontotermes* sp. with vibrational stimuli of different pulse repetition rates

	Pulse frequency (Hz)						P-value within species (N)
	8	11	14	17	20	23	
<i>M. natalensis</i> (%)	35	50	55	42	36	39	0.76 (112)
<i>Odontotermes</i> sp. (%)	55	40	45	38	56	52	0.78 (128)
P-value between species (N)	0.34 (40)	0.40 (40)	0.75 (40)	1.0 (25)	0.17 (50)	0.97 (45)	

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- a female attempts to drive away the predator (Cocroft and McNett, 2006). Giant honeybees (*Apis dorsata*) warn potential predators by producing shimmering movements. The signalling behaviour spreads from individual to individual, resulting in waves of movement across the entire (up to 1 m-wide) comb (Kastberger et al., 2008).
- It has been suggested that termite drumming is more a warning signal aimed at vertebrate predators than an alarm signal (Howse, 1984). In hymenopterans, acoustical warning signals aimed at potential predators have been described in several species (Kirchner, 1997). Bumblebees, for example, react to disturbances by producing a hissing sound. Domestic mice entering the nest of a colony retreat immediately in response to this sound (Kirchner and Röscher, 1999). In contrast to aculeate hymenopterans, termites have limited direct defence capabilities against predation from vertebrates and ants; they are mainly indirectly protected by the nest. Here, we have shown that the drumming signals are definitely used for intraspecific alarm communication. Nestmates are extremely sensitive to these vibrations and also start to drum, thereby amplifying the signal. Whether drumming signals additionally serve as warning signals aimed at predators, as Howse (Howse, 1984) suggested, remains an open question.
- The galleries of neighbouring *Macrotermes* colonies can overlap and *Macrotermes* displays a strong aggressive reaction towards non-nestmates (Jmhasly and Leuthold, 1999). Hence, drumming signals could be used for communication with neighbouring colonies to prevent expensive aggressive interactions at the boundaries of their territories. Therefore, it would be advantageous to discriminate the drumming signals of nestmates from drumming signals produced by strangers. However, we could not find any evidence that *M. natalensis* and *Odontotermes* sp. are able to discriminate between pulses of different time structure. This is in accordance with previous findings. Neither *M. bellicosus* and *M. subhyalinus* (Röhrig et al., 1999) nor *P. spiniger* and *P. militaris* (Connétable et al., 1999) are able to discriminate between vibrational stimuli with different pulse structure in the relevant range. The fact that none of these termite species discriminate between species-specific signals might also indicate that a major function is warning of predators rather than communication with intraspecific and interspecific competitors.
- Furthermore it would be advantageous if signals carried information about the direction of the signal source. Although there are several behavioural studies demonstrating the ability of insects to localise a source of vibration, there is little information about the underlying mechanisms (Cocroft, 2001; Virant-Doberlet et al., 2006; Hill, 2009). If a termite somewhere in the vast gallery system detects alarm signals, it has to make a decision to walk either in one direction or the other. Because of the low propagation velocity of surface waves it may be that time delays of the arriving substrate-borne waves between legs are used as a cue for orientation as has been demonstrated in the sand scorpion *Paruroctonus mesaensis* (Brownell, 1977).
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