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# Termites assess wood size by using vibration signals

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**Contrary to the common perception that termites are indiscriminant eaters, termites choose their food carefully; however, the methods by which they choose food are not well understood. Using choice experiments and recordings of termites feeding on wooden blocks of different sizes, we show that worker drywood termites (*Cryptotermes domesticus*) use the resonant frequency of a block of wood to assess its size. Drywood termites showed differences in their response to vibration recordings of termites compared with artificially generated signals, suggesting that they can discriminate the source of vibration. Furthermore, fewer workers matured into neotenic reproductives when recorded termite signals were played, suggesting that vibration signals play an important role in termite communication.**

foraging | vibroacoustic | communication | social insects

Termites have a reputation of being voracious and nondiscriminating feeders, consuming all wood that they find. This reputation is not deserved; in fact, termites can be highly selective feeders. Wood species palatability and hardness are important, as are defensive chemicals made by the plant (e.g., refs. 1 and 2). Yet these are not the only criteria of assessment; anecdotal accounts abound of termites not consuming a piece of palatable wood after finding it (e.g., ref. 3). Clearly, the full mechanism of how termites assess a piece of wood to eat is not a process that is well understood.

One possible parameter of concern to the termite is the quantity of food. Different termite species that live in the same habitat feed on particular sizes of wood, some species targeting smaller fallen twigs and sticks and others targeting large fallen branches or entire trees. Presumably, they do this to avoid competition, but how do termites measure the size of a piece of wood? Termites come into contact with a small part of any one piece of wood and decide to eat it based on this minor contact. The decision to eat a piece of wood is made by the termites before the piece of wood is measured physically (4, 5). They do not pace linear dimensions, which would expose them to predators. Nor can they evaluate their food visually, because the worker termites are blind (6–8).

The possibility that termites could be using vibroacoustic signals to assess wood size has not, to our knowledge, been investigated. This possibility was suggested by Lenz (4), who found that *Cryptotermes* termites quickly responded to the volume of food they were given, without having any possibility of measuring the food physically. Worker termites have several types of organs that sense vibrations at the base of the antennae and on the tibiae (6–10). We know that they have the ability to hear, interpret, and use vibroacoustic signals because soldier termites generate alarm signals acoustically by drumming their heads against the substrate or shaking bodies held firmly to the substrate (6–13). Worker termites are very noisy insects: their loud chewing was mentioned by Pliny the Elder 2,000 years ago (14). This loud chewing generates acoustic emissions that have been proposed to be a method of detecting cryptic attack (15–17). Thus, it seemed plausible that worker termites might be able to detect vibration/acoustic signals generated by their foraging and use these signals to determine food quantity.

## Methods

**Food Size Preferences.** We tested the possibility that termites had food size preferences and that they could detect food sizes without physically measuring the size of the food in bioassays using pairs of wooden blocks. We used seasoned, air-dried *Pinus radiata* wood, with a cross-sectional area of 20 × 20 mm. Pairs of blocks were cut sequentially so that the blocks in each pair would be as similar to each other as possible. There were two possible lengths, 20 or 160 mm, which were arranged in three treatments (Fig. 1): treatment 1, 20 and 20 mm ($n$ = 16 replicates); treatment 2, 160 and 160 mm ($n$ = 16 replicates); and treatment 3, 20 and 160 mm ($n$ = 44 replicates).

The blocks were separated by ≈10 mm, with the just-cut surfaces facing one another, and then held together with aluminum foil and tape on three sides and glass on the top, thus creating a central cell (Fig. 1). Groups of 15 worker termites were placed into these cells, thus exposing them to (almost) identical 20 × 20 mm surfaces, but they were prevented from having any other contact with the wooden blocks. Groups of worker *Cryptotermes domesticus* termites from colonies in laboratory culture that had been collected from northern Australia were sealed in the central cell. The blocks were kept at 35°C and 90% relative humidity and covered with black plastic. Each day for the first 5 days the position of the termites was recorded. After this period the termites were left undisturbed under the black plastic and allowed to tunnel into the wood for another 9 days (i.e., 2 weeks in total).

**Measuring Signals.** We recorded the vibration signals produced by groups of *C. domesticus* workers of both species in blocks of pine wood that were 20, 40, 80, and 160 mm long. A 5-mm-deep hole was drilled into the top of each block into which groups of 15 termites were placed; a glass slide placed over the top of the hole contained the termites. A Brüel & Kjaer (Naerum, Denmark) 4370 accelerometer (charge sensitivity of 10.121 pC/ms$^{-2}$) was attached to the base of the wooden block under test, and this was connected to a Brüel & Kjaer 2635 charge amplifier and a Tektronix differential amplifier (AM 502). The experiment was performed in an anechoic room, and the signal was monitored by using an Ono Sokki (Yokohama, Japan) fast Fourier transform CF 350 analyzer and recorded on a personal computer for analysis with the MATLAB signal processing toolbox (MathWorks, Natick, MA).

**Signals and Food Preferences.** Results from the food size preferences experiment indicated that *C. domesticus* workers chose to tunnel into the 20-mm block. To determine whether the termites used vibration signals to measure wooden block size, we examined the influence of two of the recorded natural signals and two artificially synthesized signals on the decision-making of workers choosing wooden blocks. Groups of 15 *C. domesticus* workers were sealed between two sequentially cut blocks of pine wood, one of 20 mm and the other of 160 mm (as for treatment 3 above) for the next four treatments (Fig. 1), which were as follows:

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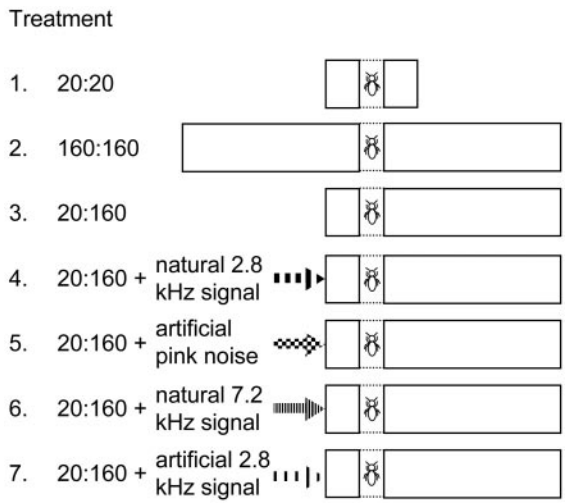


**Fig. 1.** Schematic of all experimental treatments. Treatment indicates the length of the two blocks (in mm) and the playback signal (if any). The natural 2.8-kHz signal was recorded from termites in a 160-mm block; the natural 7.2-kHz signal was recorded from termites in a 20-mm block; the artificial pink noise was energy-modulated static noise generated by a computer; the artificial 2.8-kHz signal was generated by using a computer. The termite symbol represents the 15 worker termites in the central cell.

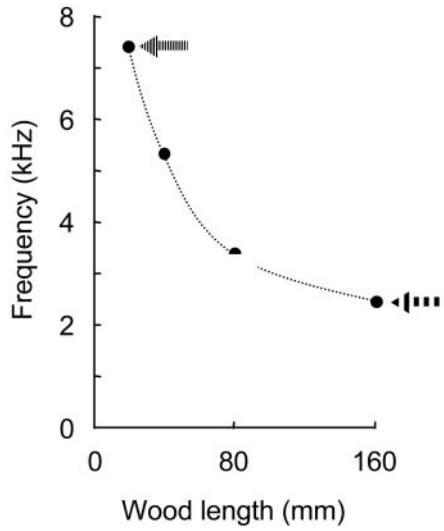


**Fig. 2.** Dominant resonant frequency of *P. radiata* wooden blocks excited by *C. domesticus* termite workers. The arrows indicate signals used in playback experiments; the shading of the arrows matches that shown in Fig. 1.

treatment 4, a 2.8-kHz signal recorded from the *C. domesticus* workers in the 160-mm blocks played into the 20-mm block ($n$ = 40 replicates); treatment 5, a pink noise (i.e., static noise in which energy across each frequency band or octave is the same) signal played into the 20-mm block ($n$ = 32 replicates); treatment 6, a 7.2-kHz signal recorded from the *C. domesticus* workers in the 20-mm blocks played into the 20-mm block ($n$ = 8 replicates); and treatment 7, an artificially generated 2.8-kHz signal equivalent to the dominant frequency recorded in the 160-mm blocks played into the 20-mm block ($n$ = 8 replicates).

Block pairs were all assembled as described above, with the just-cut, almost identical surfaces facing into the cell. However, treatments 4–7 were not assembled with glass and aluminum foil, because these materials might have transmitted some signal. Instead, the playback treatments were assembled with a 20-mm tube of thin plastic sheet. This was roughened on the base to allow for easier walking by the termites. The 20-mm wooden block was attached with a screw to a Philip Harris (Leicestershire, United Kingdom) shaker, which received the signal from a Sony (Tokyo) Discman. As for treatments 1–3, for treatments 4–7 the position of the termites was noted for the first 5 days, and after 2 weeks the experiment was stopped, the numbers of termites and holes were counted, and the depth of the tunneling into the wooden blocks was measured.

Preferences between blocks in a pair were tested by using paired $t$ tests, and differences between treatments were tested with the proportion of total tunneling activity that occurred in the 20-mm block by using ANOVA. Tunnel-length data were log-transformed to improve normality and homogeneity of variance assumptions.

## Results

**Food Size Preferences.** The termites had no preference when presented with two (almost) identical pieces of wood: similar numbers of termites were observed on both inner surfaces in treatments 1 (20:20) and 2 (160:160) during the first 5 days of observation (see Fig. 4). After 2 weeks, the termites had chewed a similar number of tunnels in each block [20:20, $t$ value with 15 df ($t_{15}$) = 0.169, $P$ = 0.868; 160:160, $t_{15}$ = 0.355, $P$ = 0.728], and these were of similar length (20:20, $t_{15}$ = 0.554, $P$ = 0.587; 160:160, $t_{15}$ = 0.684, $P$ = 0.505) (see Fig. 5).

In stark contrast, termites showed a clear preference for the 20-mm block of wood in treatment 3 (20:160). More workers were observed sitting on the 20-mm surface in the first 5 days (see Fig. 4), and after 2 weeks the termites had chewed significantly more tunnels ($t_{43}$ = 4.687, $P$ < 0.001) and significantly

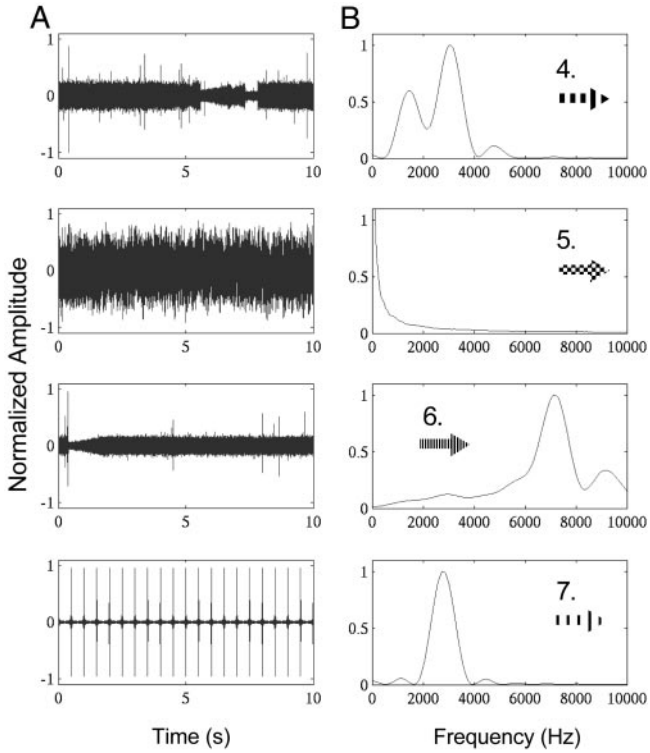


**Fig. 3.** Vibroacoustic recordings of playback treatments 4–7. (*A*) The time series signal. (*B*) The fast Fourier transform of the signal showing the frequency spectrum. The arrows indicate signals used in playback experiments; the shading of the arrows matches that shown in Fig. 1.

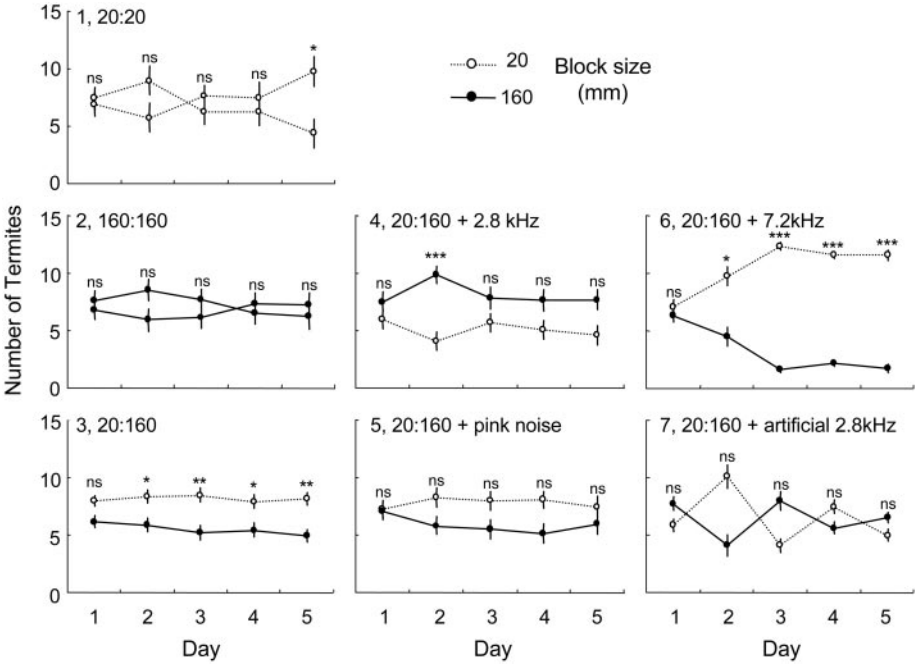


**Fig. 4.** Daily position of *C. domesticus* termite workers in the first 5 days of the experiments. Shown is the average (±standard error) number of workers in either block. Open circles and dotted line represent 20-mm blocks; filled circles and solid line represent 160-mm blocks. ns, not significant. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

deeper tunnels ($t_{43} = 2.189$, $P = 0.034$) in the 20-mm block (see Fig. 5).

**Measuring Signals.** The dominant frequency recorded from the wooden block varied inversely with block length: the frequency decreased as block size increased (Fig. 2). The time traces of two natural signals recorded from the termites, 2.8 kHz from the 160-mm block and 7.2 kHz from the 20-mm block, and the two artificial signals synthesized on computer are illustrated in Fig. 3*A*. The corresponding frequency spectra obtained by applying fast Fourier transform to the time traces are displayed (Fig. 3*B*), with the dominant frequency in the natural signals evident.

**Signals and Food Preferences.** Observation of the position of the termites on the inner surfaces during the first 5 days of the experiment showed that the termites had a clear preference for the 160-mm block when the 20-mm block was excited by the 2.8-kHz signal, a preference for the 20-mm block when it was excited by the pink noise signal, a much greater preference for the 20-mm block when it was excited by the 7.2-kHz signal, and no preference at all for either block when the 20-mm block was excited by the 2.8-kHz artificial signal (Fig. 4).

These behavioral observations were confirmed by the tunneling patterns recorded at the end of the experiment. Both the number of tunnels and the total length of tunnels, shown in Fig. 5 *A* and *B*, respectively, were higher in the 160-mm block in treatment 4 (20:160 with natural 2.8-kHz signal): number of tunnels, $t_{31} = 2.252$, $P = 0.032$; tunnel length, $t_{31} = 2.926$, $P = 0.006$. The tunneling differences were not significant in treatment 5 (20:160 with artificial pink noise signal), although nearly considering number of tunnels: number of tunnels, $t_{31} = 1.775$, $P = 0.086$; tunnel length, $t_{31} = 1.623$, $P = 0.115$. Tunneling activity was significantly higher in the 20-mm block for treatment 6 (20:160 with natural 7.2-kHz signal): number of tunnels, $t_7 = 2.049$, $P = 0.080$; tunnel length, $t_7 = 3.565$, $P = 0.009$. Finally, tunneling activity did not differ significantly in treatment 7 (20:160 with artificial 2.8-kHz signal): number of tunnels, $t_7 = 0.243$, $P = 0.815$; tunnel length, $t_7 = 0.427$, $P = 0.682$.

The lack of significant difference in tunneling activity in treatment 5 (20:160 with pink noise) suggested that random noise had the effect of changing the termite tunneling behavior, directing it away from the 20-mm block. However, an examination of the data in Figs. 4 and 5 shows that treatments 3 (20:160), 5 (20:160 with pink noise), and 6 (20:160 with natural 7.2-kHz signal) have the same pattern of higher tunneling in the 20-mm block. This pattern is supported by comparing the proportions of tunneling in the 20-mm block (Fig. 6). The proportion of the total number of tunnels differed significantly among treatments ($F_{6,149} = 4.336$, $P < 0.001$). This result was driven by the difference between treatment 4 (20:160 with 2.8-kHz signal) and treatments 3 (20:160) (Bonferroni-corrected $P < 0.001$) and 5 (20:160 with pink noise) ($P = 0.003$), as all other paired comparisons were not significantly different (although the comparison of treatments 4 and 6 was nearly so) (Fig. 6). The proportion of tunnel length in the 20-mm block differed significantly among treatments also ($F_{6,149} = 3.446$, $P = 0.003$). As for the proportion of tunnel numbers shown above, this result was driven by the difference between treatment 4 (20:160 with 2.8 kHz) and treatments 3 (20:160) (Bonferroni-corrected $P = 0.014$), 5 (20:160 with pink noise) ($P = 0.010$), and 6 (20:160 with 7.2-kHz signal) ($P = 0.017$); all other paired comparisons were not significantly different (Fig. 6).

These results were not a consequence of termite survival, because the number of survivors did not differ significantly between treatments ($F_{6,\ 149} = 1.625$, $P = 0.144$). However, the number of secondary, neotenic reproductives did differ significantly between treatments ($F_{6,\ 149} = 9.826$, $P < 0.001$). The patterns of significant difference were complex, but the most consistent differences were between treatments 4 and 6 and the remainder. Therefore, treatments were grouped into those that did not have any playback (1, 2, and 3), with an average of 4.0 ± 0.2 neotenics, those that had natural recorded signals (4 and 6), with an average of 1.8 ± 0.2 neotenics, and those that had artificially generated signals (5 and 7), with an average of 3.6 ± 0.3 neotenics. The number of survivors did

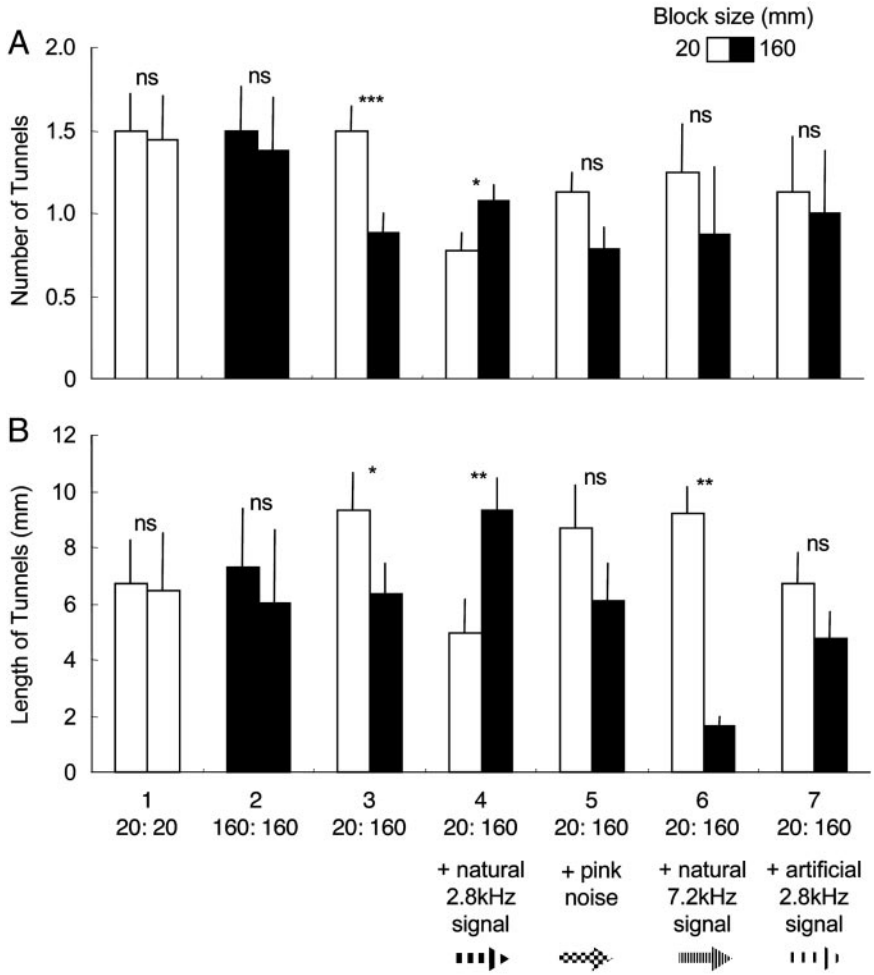


**Fig. 5.** Responses of *C. domesticus* workers to choice of wooden blocks with or without vibroacoustic signals. (*A*) Number of tunnels (average ± standard error) in paired wooden blocks. (*B*) Total length of tunnels (average ± standard error) in paired wooden blocks at the end of the experiment. Open columns, 20-mm blocks; filled columns, 160-mm blocks. ns, Not significant. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

not differ significantly among these grouped treatments ($F_{2, 153} = 1.149$, $P = 0.320$), but the number of secondary, neotenic reproductives did ($F_{2, 153} = 20.883$, $P < 0.001$). This latter difference was caused by the natural-signal grouped treatments having significantly fewer neotenics than the other two grouped treatments (Bonferroni-corrected post hoc comparisons, $P < 0.001$) and by there being no difference between the other two ($P = 0.864$).

## Discussion

Termites did not show any preference, either in sitting behavior or tunneling, between (almost) identical blocks (treatments 1 and 2). They did show a clear preference for the smaller block (treatment 3), and the only source of information available by which to differentiate between these surfaces was vibroacoustic signals that they generated and that were affected by the size of the block of wood. As would be expected, the resonant frequency of a wooden block was inversely proportional to the size of the block. When recorded signals from large or small blocks were played into the small block, the termites changed their behavior: when the signal from the large block was played, the preference either disappeared or was reversed (treatment 4), and when the signal from the small block was played, the preference was maintained and the response was increased (treatment 6). Termites did not change their behavior when pink noise, a random noise signal, was played into the small block (treatment 5), but their preference disappeared when an artificially generated signal of the dominant frequency of the large block was played into the small block (treatment 7).

These results suggest that the termites were using the dominant frequencies of the blocks to determine their sizes, but this is probably not the only information that the termites perceived, as indicated by comparing the results from the natural and artificial large-block signals (treatments 4 and 7). The termites that were played the artificial signal showed no preference for either block (160 or 20 mm with the signal), indicating that the termites perceived both blocks to be the same. The termites that were played the natural signal showed either no preference or a preference for the large block (depending on the measurement), indicating that the termites perceived the blocks differently. The difference may lie in the source of the signal: perhaps termites could perceive the termite origin of the natural signal and responded by showing some preference for the block "without" termites (i.e., the 160-mm block).

Support for the hypothesis that the termites gained information about the source of the signal comes from comparing the results from the no-signal and natural small-block signals (treatments 3 and 6). The termites showed the same pattern of response, namely, preferring the small block. However, the magnitude differed, because termites showed a greater preference for the small block with the natural signal. Perhaps the

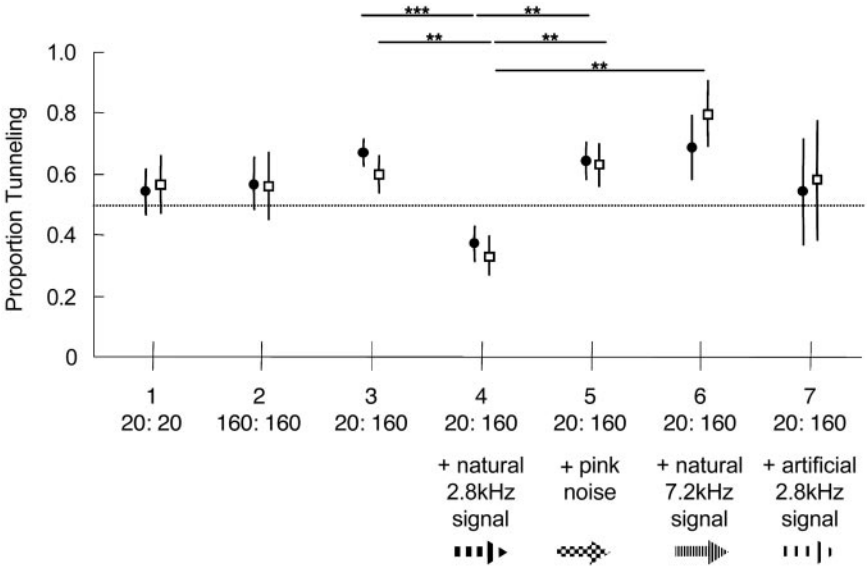


**Fig. 6.** The proportional tunneling activity of *C. domesticus* termite workers in the 20-mm blocks at the end of the experiments. Filled circles, the average (± standard error) proportion of tunnels; open squares, the average total tunnel length in the 20-mm block; for treatments 1 (20:20) and 2 (160:160), one block in each pair was chosen randomly to calculate proportion of tunneling activity for comparison with other treatments. The dotted line indicates 50% (i.e., no preference). The arrows indicate signals used in playback experiments; the shading of the arrows matches that shown in Fig. 1. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

termites, just separated from their own colony, were keen to find other termites and so directed more of their tunneling efforts in the small block with termite vibrations. The fact that termites use vibration signals in their decision-making can also be seen from the decrease in the variability of the response when a signal was played. The variance in the number of tunnels in the 20- and 160-mm blocks was higher in the no-signal group (treatments 1–3), 0.68 and 0.79, respectively, compared with that in the natural-signal group (treatments 4 and 6), 0.46 and 0.41, respectively, and in the artificial-signal group (treatments 5 and 7), 0.52 and 0.61, respectively.

Why did the *C. domesticus* termites prefer a smaller food resource over a larger one? This preference may be a response to the disturbance they endured in the experimental setup: a response to their removal from their natal colonies may be to seek shelter in the smaller piece of wood. Indeed, perhaps the preference of *C. domesticus* for smaller pieces of wood has evolved as a means of avoiding larger termites; in any case, it seems to have allowed them to survive in smaller pieces of wood, such as furniture, and thereby to be transported around the world and to become a cosmopolitan pest spread by human activities (4, 6, 18, 19).

The vibroacoustic signals described here have not, to our knowledge, been identified before now. The vibration alarm signals reported in the literature are generally <2 kHz (6–13), and acoustic emissions used to detect attack are ultrasonic (>60 kHz) (15–17). Vibration signals have been found to be important in attracting other foraging workers in eusocial Hymenoptera, including leaf-cutting ants (20, 21), which use such signals to recruit other individuals to help cut leaves, and honey bees (22, 23), which use vibrations transmitted into the honeycomb during the waggle dance to attract others. However, to our knowledge this is the first time that a vibration signal has been shown to influence the decision-making process of choosing food by termites.

Support for the hypothesis that termites get information other than wood size from vibration signals comes from the results of differing reproductive development; significantly fewer termites developed into secondary, neotenic reproductives when recorded natural signals were played, compared with artificially generated signals or no signals at all. This might be explained by the reproductive options of the workers: they can mature and reproduce directly, either as primary (i.e., winged, dispersing adults that start their own colonies) or as secondary (i.e., wingless, nondispersing neotenics that take over the existing colony) reproductives, or they can remain as workers that help the reproductives (indirect reproduction). Dispersal is dangerous, with most alates failing to establish new colonies; therefore, when enough food is available, the workers are likely to stay and try either to become secondary, neotenic reproductives or to remain as workers and help the secondary reproductives. Only with smaller food resources do workers mature into dispersing alates (4). The competition to become the neotenic reproductives is intense among *Cryptotermes* spp., with only two neotenics per colony surviving the fatal fighting (5). The decision to remain as workers depends on the information that the termites have: in the experiments here, the termites that heard the natural-signal treatments were "fooled" into believing that there were more termites and so, perhaps, were content to remain as worker-helpers.

Restriction of worker development into reproductives, neotenic or otherwise, has been reported in all eusocial insects. Restriction of development is caused by physical attack such as biting or by pheromones acting on gonad development in social wasps, bees, ants, and termites (24–27); however, to our knowledge, vibration signals have not before been implicated in affecting reproductive development. Perhaps this result should not be so unexpected: termites have many fewer pheromone-producing glands than the social hymenoptera [11 in termites compared with 14 in wasps, 21 in bees, and 39 in ants (28–30)], and perhaps vibration signals will in the future be implicated in other forms of termite interaction.

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1. Smythe, R. V. & Carter, F. L. (1970) *Ann. Entomol. Soc. Am.* **63,** 841–847.
2. Behr, E. A., Behr, C. T. & Wilson, L. F. (1972) *Ann. Entomol. Soc. Am.* **65,** 457–460.
3. Evans, T. A. (2001) *J. Econ. Entomol.* **94,** 1602–1609.
4. Lenz, M. (1994) in *Nourishment and Evolution in Insect Societies*, eds. Hunt, J. H. & Nalepa, C. A. (Westview, Boulder, CO), pp. 159–209.
5. Korb, J. & Lenz, M. (2004) *Behav. Ecol.* **15,** 390–395.
6. Grassé, P. P. (1982) *Termitologia, Tome 1: Anatomie, Physiologie, Reproduction des Termites* (Masson, Paris).
7. Grassé, P. P. (1984) *Termitologia, Tome 2: Fondation des Sociétes, Construction* (Masson, Paris).
8. Grassé, P. P. (1986) *Termitologia, Tome 3: Comportement, Socialité, Ecologie, Evolution, Systematique* (Masson, Paris).
9. Howse, P. E. (1965) *Insectes Sociaux* **12,** 335–345.
10. Kirchner, W. H., Broecker, I. & Tautz, J. (1994) *Physiol. Entomol.* **19,** 187–190.
11. Sbrenna, G., Sbrenna-Micciarelli, A., Leis, M. & Pavan, A. (1992) in *Biology and Evolution of Social Insects*, ed. Billen, J. (Leuven Univ. Press, Leuven, Belgium), pp. 233–238.
12. Connétable, S., Robert, A., Bouffault, F. & Bordereau, C. (1999) *J. Insect Behav.* **12,** 329–342.
13. Röhrig, A., Kirchner, W. H. & Leuthold, R. H. (1999) *Insectes Sociaux* **46,** 71–77.
14. Pliny, the Elder, *Naturalis Historia*, trans. Rackham, T. E. (1961) (Harvard Univ. Press, Cambridge, MA), p. 435.
15. Fujii, Y., Noguchi, M., Imamura, Y. & Tokoro, M. (1990) *Forest Prod. J.* **40,** 34–36.
16. Lemaster, R. L., Beall, F. C. & Lewis, V. R. (1997) *Forest Prod. J.* **47,** 75–79.
17. Yanase, Y., Fujii, Y., Okumura, S., Imamura, Y. & Yoshimura, T. (1998) *Forest Prod. J.* **48,** 43–46.
18. Gay, F. J. (1969) in *Biology of Termites*, eds. Krishna, K. & Weesner, F. M. (Academic, New York), pp. 459–494.
19. Su, N.-Y. & Scheffrahn, R. H. (2000) in *Termites: Evolution, Sociality, Symbioses, Ecology*, eds. Abe, T., Bignell, D. E. & Higashi, M. (Kluwer, Dordrecht, The Netherlands), pp. 437–453.
20. Roces, F., Tautz, J. & Hölldobler, B. (1993) *Naturwissenschaften* **80,** 521–524.
21. Tautz, J., Roces, F. & Hölldobler, B. (1995) *Science* **267,** 84–87.
22. Tautz, J., Rohrseitz, K. & Sandeman, D. C. (1996) *Nature* **382,** 32 (lett.).
23. Nieh, J. C. & Tautz, J. (2000) *J. Exp. Biol.* **203,** 1573–1579.
24. Kenneth, G. R. & Matthews, R. W., eds. (1991) *The Social Biology Of Wasps* (Comstock Publ. Assoc., Ithaca, NY).
25. Bourke, A. F. G. & Franks, N. R. (1995) *Social Evolution in Ants* (Princeton Univ. Press, Princeton).
26. Peeters, C. & Hölldobler, B. (1995) *Proc. Natl. Acad. Sci. USA* **92,** 10977–10979.
27. Bourke, A. F. G. (1999) *J. Evol. Biol.* **12,** 245–257.
28. Kaib, M. (1999) in *Pheromones of Non-Lepidopteran Insects Associated with Agricultural Plants*, eds. Hardie, J. & Minks, A. K. (CABI, Oxon, U.K.), pp. 329–353.
29. Hölldobler, B. & Wilson, E. O. (1990) *The Ants* (Springer, Berlin).
30. Vander Meer, R. K., Breed, M. D., Espelie, K. E. & Winston, M. L., eds. (1998) *Pheromone Communication in Social Insects* (Westview, Boulder, CO).