

Tunnel Formation by *Reticulitermes flavipes* and *Coptotermes formosanus* (Isoptera: Rhinotermitidae) in Response to Wood in Sand

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ABSTRACT The tunneling responses of two subterranean termite species, *Coptotermes formosanus* Shiraki and *Reticulitermes flavipes* (Kollar), to the presence of sound wood in laboratory arenas were studied. Branching pattern and the speed of tunnel construction between *R. flavipes* and *C. formosanus* also were compared. Patlak's residence index (ρ) was generated using the length, width, speed of construction, and area of the primary tunnels built by termites. In the same allotted time, *C. formosanus* built wider and shorter primary tunnels, whereas *R. flavipes* built thinner and longer primary tunnels. The presence of wood did not affect termite tunnel formation. This lack of variation in tunnel formation parameters was evidenced by the inability of the termites to locate wood sources over distance, even as short as 2.5 mm, and by the similar tunneling behaviors in areas of the arena with or without wood. Patlak's model predicted the densities of tunnels with an error between 9 and 28%, in experiments with *R. flavipes* exposed to a range of 0–8,000 g of wood, and between 61 and 87% in experiments with *C. formosanus*. These results indicated that the residence index can provide a qualitative measure of the effect of habitat heterogeneity on the individual termite tunnels. The tunneling construction strategy of these subterranean termites is discussed.

KEY WORDS *Reticulitermes flavipes*, *Coptotermes formosanus*, termite tunneling, termite foraging, termite behavior

THE TUNNELING BEHAVIOR of subterranean termites is difficult to study due to their cryptic habitat. These termites build an intricate network of tunnels in soil, connecting nesting sites and wood, and movement of the termite workers away from their reproductive centers via foraging tunnels is a key element in their population ecology. However, few attempts have been made to discern the causes that may compel the workers to seek food sources. The complexity and sizes of the network of underground tunnels (King and Spink 1969) and the mathematical constraints to analyze such data (Skellam 1951, 1973) have interfered with the study of subterranean termites in their habitat.

The eastern subterranean termite, *Reticulitermes flavipes* (Kollar), and the Formosan subterranean termite, *Coptotermes formosanus* Shiraki, are the two most economically important subterranean termite species in the United States (Su and Scheffrahn 1990). Recent developments for control of subterranean termites include the use of monitoring-baiting programs (Su 1994). In such programs, monitoring stations are first placed in the soil and then replaced with toxic bait when termites are detected in the wood in the monitoring stations. Usually, some monitoring stations are infested by termites over time and the colony is eliminated by subsequent bait application (Su and Scheffrahn 1998), but only a few stations are intercepted by termites.

Several studies (Smythe et al. 1967, Amburgey and Smythe 1977) suggested that subterranean termites are attracted to substances that emanate from decayed

wood and termites orientated to this chemical plume and followed it to the wood. At present, little is known about the mechanisms by which termites locate wood in the soil.

We wanted to determine whether the tunneling response of the subterranean termites *R. flavipes* and *C. formosanus* differed in soil containing or lacking wood, and to compare the branching pattern and the speed of tunnel construction between these two species. We adopted the mathematical framework postulated by Patlak (1953) that used four parameters (μ , mean tunnel length; M , mean squared tunnel length; τ , duration of tunnel construction, and ψ , mean cosine of the turning angle) to study the effects that the presence of wood had on termite tunneling and their relative spatial distribution.

Materials and Methods

R. flavipes and *C. formosanus* were collected from field colonies in Broward County, FL, by using the method described by Su and Scheffrahn (1986).

Termite Tunneling in Foraging Arena. Experimental arenas were constructed of two sheets of transparent Plexiglas (105 by 105 cm) separated from each other by four Plexiglas laminas (105 by 2.5 by 0.2 cm) placed between the outer margins (Fig. 1). The upper sheet had five chambers (6.5 cm in diameter by 8.0 cm in height, covered with 7.0-cm-diameter Plexiglas lid) with clusters of four access holes (1 cm in diameter). Four chambers were equidistantly separated 30 cm

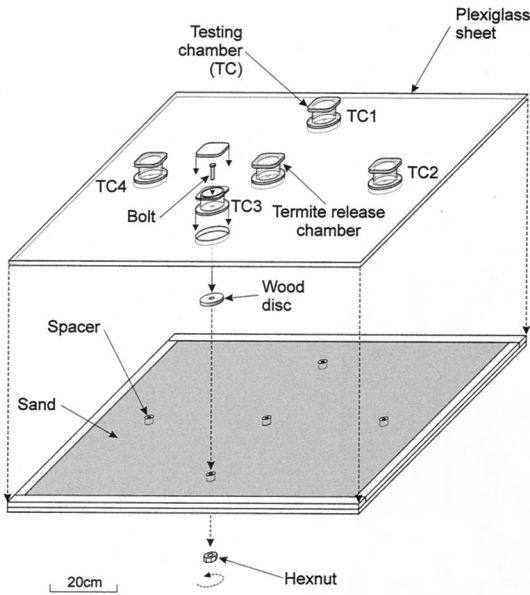


Fig. 1. Experimental arena constructed of two sheets of transparent Plexiglas, separated from each other by Plexiglas laminas placed between the outer margins

from a center chamber (Fig. 1). The center chamber was used to release termites and the other four represented potential foraging destinations or testing chambers (TCs) designated as TC1–TC4 clockwise. The perimeters of the experimental arenas were held together with binder clips.

The 0.2-cm gaps between the Plexiglas sheets were filled with 2.1–2.4 kg of sifted sand (150–500- μm sieves; Play Sand Bonsal, Miami, FL) and moistened with 500–600 ml of deionized water. The testing disk (6.5 cm in diameter by 0.3 cm in thickness with a 0.5-cm-diameter hole at the center). Disks were secured through the center hole between the arena gaps beneath the four access holes of the testing chamber by a screw (0.5-cm-diameter hole). The mean \pm SD dry weight of each wooden disk (2.2166 ± 0.1995 g) was determined by drying at 38°C for 24 h in a desiccator before weighing.

After each experiment was run, three samples of moist sand were collected from each experimental arena, weighed, and dried for 24 h at 38°C, and reweighed to estimate the approximate moisture content in the sand, which was $22.2 \pm 5.46\%$ (mean \pm SD).

A group of 1,000 workers (undifferentiated larvae of at least the third instar) plus 100 soldiers and 10 soldiers of *C. formosanus* and *R. flavipes*, respectively (Su and La Fage 1987, 1999), were released in the center chamber containing wooden sticks of 3 cm in length. Six experiments were run simultaneously, three each for *R. flavipes* (R1, R2, and R3) and for *C. formosanus* (C1, C2, and C3). Experiments R1 and C1 represented control conditions and no wood was placed beneath any of the four testing chambers. For experiments R2 and C2, two testing chambers (TC3 and TC4) received wooden disks. In experiments R3 and C3, all

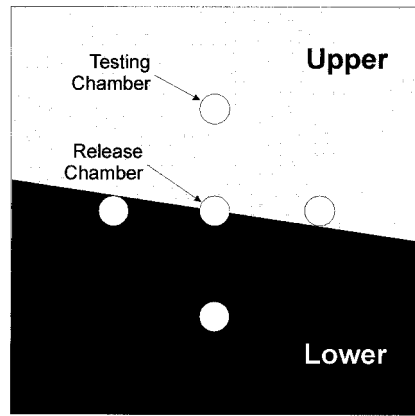


Fig. 2. Regions of interest in the experimental arena: upper (without wood) and lower (with wood) quadrants.

four testing chambers received wooden disks. The wooden disks in these experiments were embedded and in contact with the substrate (sand). All the experiments were conducted with the arenas in the horizontal position in a dark room at $27^\circ\text{C} \pm 2^\circ\text{C}$. Five replicates (colonies) of each experiment were conducted ($n = 3$ treatments \times five replicates = 15 experimental units) for each termite species.

Termite tunnels were recorded daily for ≈ 10 d, or until termites reached the edges of the arenas. Tunnels were traced daily by using different colors on a transparent plastic sheet placed on top of the experimental arenas. A digital photograph was taken of each of the resulting tunnels and the digital images were downloaded into the computer for later analysis (Picture Easy; Kodak Digital Science, Rochester, NY).

Tunnels were designated as two classes: primary or secondary. Tunnels originating from the release chamber were classified as primary. Tunnel branching from the primary tunnel were classified as secondary (Selkirk 1982). Tertiary and quaternary tunnels were included in the secondary class.

We measured the length of primary tunnels (the longest length of the primary tunnels constructed from the release chamber) (d), the distance of primary tunnels from the release chamber to the first secondary-tunnel originated (do), the length of the secondary tunnels (db), and the width (W) of the tunnels. Sigma Scan Pro (SPSS software, version 4.0) was used to measure these variables.

The total distance traveled ($TD = d + db$); the area occupied ($A = TD \times W$); the density inside the tunnels ($D = NW/A$, where NW is the number of workers released); and the speed of tunnel growth ($S = TD/t$, where t is the time used to run the experiment (6 to 10 d) were calculated. Because half of the testing chambers were loaded with wood for R2 (*R. flavipes*) and C2 (*C. formosanus*), we divided these arenas in two quadrants: the upper quadrant without wood and the lower quadrant with wood. Measurements were taken in the upper and lower quadrants of these arenas (Fig. 2).

Table 1. Comparison of parameters (\pm SD) measured in tunnel construction trials with *C. formosanus* and *R. flavipes*

Exp.	<i>a</i> (cm)	<i>W</i> (cm)	<i>S</i> (cm/day)	<i>A</i> (cm ²)	<i>db</i> (cm)	<i>TD</i> (cm)	<i>do</i> (cm)
<i>R. flavipes</i>							
R1	498.4 \pm 482.5a	0.441 \pm 0.082a	130.5 \pm 129.8a	443.9 \pm 478.3a	492.9 \pm 676.2a	991.3 \pm 1021.8a	86.8 \pm 144.9a
R2	501.9 \pm 469.3a	0.440 \pm 0.081a	126.2 \pm 136.2a	404.4 \pm 389.4a	437.7 \pm 579.2a	939.5 \pm 959.3a	96.9 \pm 132.3a
R3	379.7 \pm 330.7ac	0.540 \pm 0.272a	104.7 \pm 93.2a	472.7 \pm 636.5a	390.9 \pm 426.6a	770.7 \pm 696.0a	80.5 \pm 109.1a
<i>C. formosanus</i>							
C1	233.4 \pm 218.2bc	1.739 \pm 0.770b	67.4 \pm 63.7b	913.7 \pm 1010.5b	272.5 \pm 372.1a	505.9 \pm 484.6a	28.4 \pm 35.7a
C2	288.1 \pm 287.6bc	1.706 \pm 0.745b	80.8 \pm 68.4b	1197.2 \pm 1440.1b	316.7 \pm 348.4a	604.8 \pm 523.1a	37.8 \pm 66.5a
C3	237.0 \pm 314.3b	1.422 \pm 0.645b	79.0 \pm 95.5b	948.0 \pm 1187.7b	354.7 \pm 596.2a	591.7 \pm 705.4a	30.9 \pm 71.2a

d, Length of primary tunnels built; *W*, width of the tunnels built; *S*, speed of tunnel construction; *A*, area occupied; *db*, the length of secondary tunnels; *TD*, total distance of tunnels constructed; *do*, initial distance to first branch built by *R. flavipes* (R1 [no wood], R2 [two of four testing chambers with wood], and R3 [four testing chambers with wood]) and *C. formosanus* (C1 [no wood], C2 [two of four chambers with wood], and C3 [four chambers with wood]) in experimental arenas. Means in the same column followed by different letters are significantly different (ANOVA, $P < 0.05$).

Comparison of Tunneling by *C. formosanus* and *R. flavipes*. We regrouped the data (1) by wood presence (we compared experiments without wood, R1 or C1, with experiments with wood in all testing chambers, R3 or C3, and in experiments R2 and C2, where two of the four testing chambers contained wood we compared the upper quadrant [no wood] with the lower quadrant [with wood]); and (2) by time (before and after reaching any testing chamber). The arena was held horizontally and the upper or lower quadrant implies the relative position of a region of the arena and does not imply the gravitational orientation of the quadrant.

An analysis of variance (ANOVA) was used to detect significant differences ($P < 0.05$) in the length of primary tunnels (*d*), width of the tunnels (*W*), speed of tunnel construction (*S*), area occupied (*A*), length of secondary tunnels (*db*), total length of tunnel constructed (*TD*), initial distance from the primary tunnel to the first branch (*do*), and to detect differences between species and the effect of the presence of wood in the experiments (Table 1).

Number of Tunnels Intercepting a Testing Chamber. We recorded the number of tunnels intercepting a testing chamber in relation to the presence of wood. A sign test for independent samples was used to compare results between experiments without wood (R1 for *R. flavipes* and C1 for *C. formosanus*) and with wood (R3 for *R. flavipes* and C3 for *C. formosanus*). A Cochran Q-test for related samples was used to compare tunnels intercepting a testing chamber with wood and without wood (experiments R2 for *R. flavipes* and C2 for *C. formosanus*) (Table 2).

Correlated Random Walk. Patlak's diffusion approximation of correlated random walk (Patalak 1953) was used to calculate the spatiotemporal density of tunnels and to determine how this density changes with time in response to the presence of wood in the arena. This model was chosen because of its generality, flexibility, and tractability (Turchin 1991). The model can be used in more than one dimension, the direction of movement at any given time can be influenced by the direction of future movement, and the model does not assume that the speed and the turning frequency are constant.

To determine the parameters of the model, we measured the path made by the tunneling termites. A path was characterized by the tunnel length, direction, and duration. We estimated four movement parameters: the mean tunnel length (μ_j), the mean squared tunnel length (M_j), the mean duration of tunnel construction (τ_j), and the mean cosine of the turning angle (ψ_j) for each wood-time group, separately, whereas, $\mu_j = 1/n_j \sum l_{ij}$ (where l_{ij} is the length of the *i*th tunnel built in group *j*, and n_j is the total number of steps to build the tunnel in the group *j*), $M_j = 1/n_j \sum l_{ij}^2$, $\tau_j =$ total time in the quadrant divided by the number of steps needed for tunnel construction that the termites made during that period, and $\psi_j = 1/n_j \sum \cos \Phi_{ij}$.

We calculated the following quantities from Patlak's model: $\gamma = M_j / \mu_j^2$ (and took the average of the quadrant-time combination to be compared); $\phi_j = \gamma + (2 - \gamma) \psi_j$; the exponent $\alpha = (2 \gamma (\mu_2 - \mu_1)) / ((2 - \gamma) (\phi_1 \mu_2 - \phi_2 \mu_1))$, the residence index, $\rho_j = \tau_j \phi_j \alpha \mu_j - (((2-2\gamma) / (2 - \gamma)) + \alpha)$; the predicted ratio of

Table 2. Comparison of mean numbers of termite tunnels intercepting a chamber between the arena in which none of the four chambers contain wood (R1, C1) and the arenas in which all of the chambers contained wood (R3, C3), and between wood-containing and no-wood containing chambers in the arena where two of the four chambers contained wood (R2, C2)

Termite	R1, C1	R3, C3	Sign test, <i>P</i>	R2		Cochran Q-test	
	(4 chambers without wood)	(4 chambers with wood)		(2 chambers with wood, and 2 without wood)		<i>Q</i>	<i>P</i>
<i>R. flavipes</i>	2.2 \pm 1.3a	2.6 \pm 1.3a	0.812	0.8 \pm 0.8a	0.8 \pm 0.8a	3.000	>0.05
<i>C. formosanus</i>	0.6 \pm 0.9a	0.4 \pm 0.5a	0.250	1.2 \pm 1.5a	1.0 \pm 0.0a	6.667	>0.05

R, *R. flavipes*; C, *C. formosanus*.

Means in the same row followed by the same letter are not statistically different (Sign test or Cochran Q-test, $P > 0.05$).

tunnel population densities between two wood-time combinations: $\mu_{\text{after}}/\mu_{\text{before}} = \rho_{\text{after}}/\rho_{\text{before}}$.

The residence index (ρ_j) within the habitat can be used to predict the spatial distribution of the organisms as a result from their movement (Patlak 1953). To summarize the effect that the presence of wood had on termites' tunneling construction, we used the residence index of a spatial region, in our study the area searched before or after reaching a testing chamber. Low residence index indicates that the termites are passing quickly through the region at certain times, either because they increased their speed of tunnel construction or because they are making linear tunnels, or both, resulting in sparse tunnels in the arena (Turchin 1991). In contrast, a high residence index implies that the termites linger there, their speed of movement is low, they make frequent turns, and they accumulate in the area, resulting in dense distribution of tunnels in the arena (Turchin 1991). The ratio of residence indexes ($\rho_{\text{after}}/\rho_{\text{before}}$) was used to determine the effect that the presence of wood had on termite tunneling. The speed of tunnel construction was calculated as, $\text{speed} = \mu/\tau$. The sum of the speeds of two experiments (or quadrants) to be compared was considered 100% speed, and the respective percentage of speed for each experiment (or quadrant) was calculated (R1 [no wood] against R3 [with wood]; C1 [no wood] against C3 [with wood]; and in R2 and C2, we compared the upper quadrant [no wood] against the lower quadrant [with wood]).

Data Analysis and Statistical Methods. Data were tested for normality and homoscedasticity before performing ANOVA (Sokal and Rohlf 1981). The least significance difference test, Statview, was used to determine significant differences ($P < 0.05$) between treatments (SAS Institute 1998). An ANOVA was used to compare variables among the six experiments (R1, R2, and R3, C1, C2, and C3). The approximate test of equality of means was used to detect whether differences existed among the variables evaluated (Sokal and Rohlf 1981). The probability of type II error, β , was computed to be equal to 0.3 (Marks 1982).

Results and Discussion

Difference in Tunneling Distance between *R. flavipes* and *C. formosanus*. *R. flavipes* built longer ($F = 4.918$, $df = 5$, $P = 0.003$) and narrower ($F = 119.6$, $df = 5$, $P = 0.0001$) primary tunnels (Table 1), at a faster rate ($F = 11.9$, $df = 5$, $P = 0.0001$), and occupied a smaller area ($F = 11.6$, $df = 5$, $P = 0.0001$) than *C. formosanus*.

The variables db (length of secondary tunnels; $F = 1.120$, $df = 5$, $P = 0.3525$), TD (total distance; $F = 2.149$, $df = 5$, $P = 0.0633$), and d_0 (length of primary tunnel to first branch; $F = 1.802$, $df = 5$, $P = 0.1163$) did not differ among the six experiments with different configurations of wood placement and termite species (R1, R2, R3, C1, C2, and C3) (Table 1).

Number of Tunnels Intercepting a Testing Chamber. The presence of wood did not influence the number of tunnels intercepting a testing chamber for *R.*

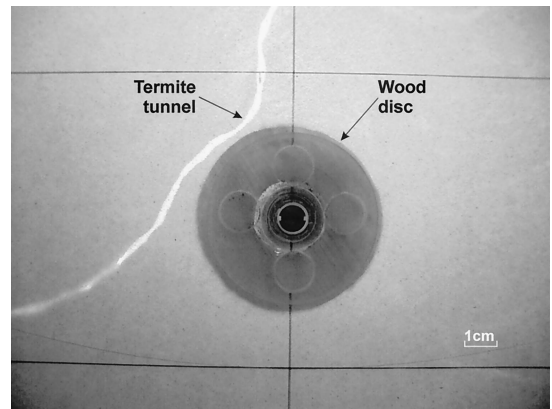


Fig. 3. Inability of the termites to recognize location of wood sources (circle) even as short a distance as 2.5 mm from wood source.

flavipes or for *C. formosanus* (Table 2). The mean number of events of testing chamber interception was not significantly different between arenas without wood (R1: 2.2 ± 1.3) or with wood (R3: 2.6 ± 1.3) ($P = 0.812$) for *R. flavipes*, nor for arenas without wood (C1: 0.6 ± 0.9) or with wood (C3: 0.4 ± 0.5) for *C. formosanus* ($P = 0.250$). The Cochran Q-test for related samples revealed that all four testing chambers had the same number of interceptions by *R. flavipes* or by *C. formosanus* in the arena (R2, C2) where two of the four chambers contained wood (Table 2). The similar rate of interceptions of chambers with different amounts of wood is another indication that these subterranean termites did not detect wood over distance. They appeared to intercept the testing chambers by chance regardless of the presence of wood. The analysis results agree with our observations that on several occasions, termite tunnels were built as close as 2.5 mm to the wooden disc without intercepting it (Fig. 3).

Correlated Random Walk Model. Termite tunneling was not affected by the presence of wood placed in the arenas (Table 3). In all the experiments (R1, R2, R3, C1, C2, and C3), the mean tunnel length, μ , before reaching a testing chamber, was not significantly different from that after reaching chambers (Kruskal-Wallis ANOVA, for *R. flavipes*: $H = 1.988$, $df = 3$, $P > 0.05$; for *C. formosanus*: $H = 2.040$, $df = 3$, $P > 0.05$). The average ratio of residence indexes ($\rho_{\text{after}}/\rho_{\text{before}}$) for each experiment (R1, R3, C1, and C3) and/or quadrant (R2 and C2 upper [U] and lower [L] quadrants), were presented in Table 3. The values for the residence indices and the ratio of residence indices among experiments were not statistically different (Approximate Test of Equality of Means, $P > 0.05$) among any treatments and between both termite species. The lack of statistical difference is an indication that, at least under the study conditions, *R. flavipes* and *C. formosanus* cannot detect wood over distance, reacting similarly under different wood and time configurations and resulting in similar residence indexes in areas of the arenas with different wood placements.

Table 3. Estimated CRW parameters for *R. flavipes* (R1, no wood; R2, two chambers with wood; R3, four chambers with wood) and *C. formosanus* (C1, no wood; C2, two chambers with wood; and C3, four chambers with wood)

Quadrant		b/a ^a	μ	τ	ψ	% speed	Mean γ	Residence index (ρ)	Avg. ρ _{after} /ρ _{before}
R1 (no wood)	Both	b	30.045a	0.007	-0.008	53.50	1.502	2.26 × 10 ⁻⁵ a	—
		a	34.855a	0.010	-0.039	45.00	—	3.02 × 10 ⁻⁵ a	1.630a
		b	30.615a	0.003	-0.025	55.55	1.761	7.47 × 10 ⁻⁴ a	—
R3 (with wood)	Both	a	28.188a	0.003	-0.024	48.90	—	48.08 × 10 ⁻⁴ a	—
		b	33.380a	0.018	0.066	27.56	1.518	3.09 × 10 ⁻⁵ a	3.071a
	Upper (no wood)	a	34.122a	0.007	0.014	72.44	—	118.77 × 10 ⁻⁵ a	—
		b	31.836a	0.002	0.046	69.76	1.587	32.67 × 10 ⁻² a	0.847a
R2	Lower (with wood)	a	34.494a	0.005	0.022	30.24	—	7.56 × 10 ⁻² a	—
		b	40.490a	0.004	-0.041	87.00	1.590	2.69 × 10 ² a	0.232a
C1 (no wood)	Both	a	38.290a	0.025	0.046	13.02	—	5.31 × 10 ² a	1.926a
		b	37.500a	0.010	0.024	27.94	1.533	1.12 × 10 ⁰ a	—
C3 (with wood)	Both	a	42.920a	0.005	-0.034	72.06	—	1.47 × 10 ⁰ a	—
		b	28.31a	0.004	-0.010	71.39	1.013	2.93 × 10 ⁻⁶ a	1.565a
	Upper (no wood)	a	56.72a	0.020	0.059	28.61	—	2.89 × 10 ⁻⁶ a	—
b		29.11a	0.003	0.014	62.06	0.923	3.23 × 10 ⁻⁶ a	1.077a	
C2	Lower (with wood)	a	59.32a	0.010	0.039	37.94	—	2.88 × 10 ⁻⁶ a	1.960a

Means followed by the different letters are statistically different (Approximate Test of Equality of Means, *P* < 0.05).
^a Number of days before (b) and after (a) reaching any testing chamber.

Comparison of Predicted and Observed Distributions. For *R. flavipes*, the model underpredicted the observed ratio of densities of termite tunnels with an error of 29% in the R1 treatment (four testing chambers empty), and underpredicted the observed densities of tunnels by 19% in the R3 treatment (four testing chambers with wood) (Table 4). The behavior of *R. flavipes* to follow the shape of the wooden disk may explain the inability of the model to predict correctly the densities of tunnels built under these conditions (see below). In the R2 treatment (two of four testing chambers with wood), the model underpredicted the observed ratio of densities of tunnels by 10% in the upper quadrant (no wood), which is within the <10% error, a commonly accepted goal in comparisons of this kind (Kareiva 1982, Turchin 1991), and predicted the observed ratio of tunnel densities by 22% in the lower quadrant (with wood) (Table 4).

For *C. formosanus*, the predicted ratio of primary tunnels was close to 1 in C1 (four testing chambers empty) and C3 (all four testing chambers with wood) treatments (Table 4), indicating that the density of tunnels was about the same between times. The model underpredicted the densities of tunnels by 61%, in both experiments (C1 and C3), indicating that the presence of wood in the arena (C3) did not affect the tunneling behavior of *C. formosanus* resulting in similar densities of tunnels in arenas with (C3) or without (C1) wood. In the C2 treatment (two of four testing chambers with wood), the model underpredicted the densities of tunnels by 87 and 85% in the upper (no wood) and lower (with wood) quadrants, respectively (Table 4). This failure of the model must be due to the tunneling behavior of *C. formosanus*. This species spends more time widening its tunnels immediately after release in the arenas contrary to *R. flavipes*,

Table 4. Comparison between the model predictions and the study results for *R. flavipes* (R1, no wood; R2: two chambers with wood; and R3, four chambers with wood) and *C. formosanus* (C1, no wood; C2, two chambers with wood; and C3, four chambers with wood)

Experiment	Quadrant	Density of primary and secondary tunnels		Observed ratio	Predicted ratio μ _{before} /μ _{after}	Error ^b
		b ^a	a			
R1	Both (no wood)	30.20 ± 3.39	24.90 ± 2.97	1.21	0.86	-28.73
R3	Both (with wood)	25.00 ± 1.31	18.60 ± 8.20	1.34	1.08	-19.19
R2	Upper (no wood)	28.40 ± 14.81	26.20 ± 17.82	1.08	0.97	-9.76
	Lower (with wood)	19.60 ± 4.22	26.00 ± 16.97	0.75	0.92	22.43
C1	Both (no wood)	17.10 ± 0.14	6.30 ± 2.12	2.71	1.06	-61.04
C3	Both (with wood)	17.70 ± 1.27	7.80 ± 0.57	2.27	0.87	-61.50
C2	Upper (no wood)	20.60 ± 15.11	5.40 ± 3.36	3.81	0.50	-86.92
	Lower (with wood)	19.00 ± 7.71	5.80 ± 3.70	3.27	0.49	-85.02

^a Number of days before and after reaching any testing chamber.
^b Error = 100 × ((predicted ratio - observed ratio)/observed ratio).

which elongates its tunnels immediately after release. Evidently, the model does not contemplate this time lag in its calculations and the time lag must be a factor affecting the predictive nature of the model.

The most conspicuous feature in the tunnel formation of the subterranean termites was that the presence of a piece of sound wood did not seem to affect termite movement to any measurable degree. Termites lack of response at the presence of sound wood was evidenced by the inability of the termites to recognize the location of wood over distance (even as short as 2.5 mm; Fig. 3), and by the contentions of finding similar tunneling behaviors in areas of the arena with or without wood. These results are in direct contrast to Goldberg (1973) and Reinhard et al. (1997) who provided evidence that sound wood was detected by *Reticulitermes* spp. over distance by volatiles emanating in open air from wood. In the current study, the wood was embedded and in contact with the sand that filled the arenas, and thus the potential volatiles suggested by Reinhard et al. (1997) may have not permeated through sand.

The subterranean termites have a parsimonious tunneling behavior that conveys them with a strategy to exploit wood sources in their search for food. This strategy differs between termite species. In the same allotted time, *C. formosanus* built wider and shorter primary tunnels than *R. flavipes*, whereas the latter built thinner and longer primary tunnels. Because *C. formosanus* consumes a greater percentage of wood before foraging to another food source than *R. flavipes* (Delaplane and La Fage 1989), this strategy of excavating wider tunnels when released in the arena may be a way for *C. formosanus* to consume wood tenaciously near the release chamber. The strategy of *R. flavipes* is to build long and narrow tunnels continuously to increase the probability of finding other wood sources.

Patlak's model predicted the densities of tunnels with >70% accuracy in experiments with *R. flavipes* (R1, four testing chambers empty; R2, two of the four chambers with wood; and R3, four testing chambers with wood). The tunneling formation strategy of *R. flavipes* consisted of passing quickly through a region and keeping their speed of construction even after finding wood. Search for food in *Reticulitermes* spp. is organized by chemical trails secreted from the abdominal sternal gland (Reinhard and Kaib 2001), with recruitment and foraging controlled by different concentrations of trail pheromone (Grace 1988, 1995). Even though Patlak's model under predicted the density of tunnels in experiments with *C. formosanus*, it gave an excellent approximation of the kind of strategy that this termite species would use after finding wood. This strategy of *C. formosanus* promoted the tunneling behavior around the sources of wood (C2, lower quadrant, with wood). As a result, tunnels irradiated from the new wood source. In situations where wood was absent in the arena (C1), termite tunnel density remained the same after reaching a testing chamber. At a certain time and distance, when the termite tunnel

density decreased, the speed of tunnel construction also decreased.

Limitations of the Model. Most of the limitations of Patlak's model were overcome by our experimental design. The model assumes that organisms do not circle or spiral. In our study, termites tended to trace the edge of circular wooden disks in the testing chamber, a behavior known as guideline-following (Jander and Daimer 1974). This behavior would lead to an increase in the residence times, with a consequent increase in the residence index. The possible increase of residence time due to the guideline-following behavior would explain the deviation between the predicted residence index and the observed ones in some of our experiments.

The model assumes that the testing units (in our case, an experimental arena) have negligible interactions with each other. Because all six experiments (testing units) were isolated from each other, there was no interaction between individual groups. The model also assumes that tunnel formation is unaffected by compass direction and that there is no long-distance attraction. In our study, there was no evidence of any influence by compass direction nor of any attraction to quadrants with wood.

We quantified termite movement with only four parameters: μ (mean tunnel length), M (mean squared tunnel length), τ (duration of tunnel construction), and ψ (mean cosine of the turning angle). We also compared the effect that the presence or absence of wood had on the termite's movement, and on their spatial redistribution. With these parameters, we calculated the residence index, ρ , which is a relative measure of the average time that an organism spends between entering and leaving a unit area that is characterized by a particular combination of tunnel formation parameters (Turchin 1991). Therefore, the residence index can be used to examine how other environmental factors affect the termite's tunnel spatial redistribution.

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References Cited

- Amburgey, T. L., and R. V. Smythe. 1977. Shelter and tube construction and orientation by *Reticulitermes flavipes* in response to stimuli produced by brown-rotted wood. *Sociobiology* 3: 27-34.
- Delaplane, K. S., and J. P. La Fage. 1989. Foraging tenacity of *Reticulitermes flavipes* and *Coptotermes formosanus* (Isoptera: Rhinotermitidae). *Sociobiology* 16: 183-189.

- Goldberg, J. 1973. Reactions du termite de saintonge aux obstacles poses pendant la construction. *Rev. Comp. Anim.* 7: 323–326.
- Grace, J. K., D. L. Wood, and G. W. Frankie. 1988. Trail following behavior of *Reticulitermes hesperus* Banks (Isoptera: Rhinotermitidae). *J. Chem. Ecol.* 14: 653–667.
- Grace, J. K., D. L. Wood, I. Kubo, and M. Kim. 1995. Behavioral and chemical investigation of trail pheromone from the termite *Reticulitermes hesperus* Banks (Isopt., Rhinotermitidae). *J. Appl. Entomol.* 119: 501–505.
- Jander, R., and K. Daimer. 1974. Guide-line and gravity orientation of blind termites foraging in the open (Termitidae: Macrotermes, Hospitalitermes). *Insectes Soc.* 21: 45–69.
- Kareiva, P. 1982. Experimental and mathematical analyses of herbivore movement: quantifying the influence of plant spacing and quality on foraging discrimination. *Ecol. Monogr.* 52: 261–282.
- King, E. G., and W. T. Spink. 1969. Foraging galleries of the Formosan subterranean termite, *Coptotermes formosanus*, in Louisiana. *Ann. Entomol. Soc. Am.* 62: 536–542.
- Marks, R. G. 1982. *Analyzing Res. Data. The Basics of Biomedical Res. Methodology.* LifeTime Learning Publications, Belmont, CA.
- Patlak, C. S. 1953. Random walk with persistence and external bias. *Bull. Math. Biophysiol.* 15: 311–338.
- Reinhard, J., H. Hertel, and M. Kaib. 1997. Systematic search for food in the subterranean termite, *Reticulitermes santonensis* De Feytaud (Isoptera, Rhinotermitidae). *Insectes Soc.* 44: 147–158.
- Reinhard, J., and M. Kaib. 2001. Trail communication during foraging and recruitment in the subterranean termite *Reticulitermes santonensis* De Feytaud (Isoptera, Rhinotermitidae). *J. Insect Behav.* 14: 157–171.
- SAS Institute. 1998. *Statview, user's reference manual*, 2nd. SAS Institute, Cary, NC.
- Selkirk, K. E. 1982. *Pattern and place, an introduction to the mathematics of geography.* Cambridge University Press, New York.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* 38: 196–218.
- Skellam, J. G. 1973. The formulation and interpretation of mathematical models of diffusional processes in population biology, pp. 63–85. *In* M. S. Bartlett and R. W. Hiorns (eds.), *The mathematical theory of the dynamics of biological populations.* Academic, London.
- Smythe, R. V., H. C. Coppel, S. H. Lipton, and F. M. Strong. 1967. Chemical studies of attractants associated with *Reticulitermes flavipes* and *R. virginicus*. *J. Econ. Entomol.* 60: 228–233.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry.* Freeman, New York.
- Su, N.-Y. 1994. Field evaluation of a hexaflumuron bait or population suppression of subterranean termites (Isoptera: Rhinotermitidae). *J. Econ. Entomol.* 87: 389–397.
- Su, N.-Y., and R. H. Scheffrahn. 1986. A method to access, trap and monitor field populations of the Formosan subterranean termite (Isoptera: Rhinotermitidae) in the urban environment. *Sociobiology* 12: 299–304.
- Su, N.-Y., and R. H. Scheffrahn. 1990. Economically important termites in the United States and their control. *Sociobiology* 17: 77–94.
- Su, N.-Y., and R. H. Scheffrahn. 1998. Elimination of subterranean termite populations from the statue of liberty National Monument using bait matrix containing an insect growth regulator, hexaflumuron. *J. Am. Inst. Conserv.* 37: 282–292.
- Su, N.-Y., and J. P. La Fage. 1987. Effects of soldier proportion on the wood-consumption rate of the Formosan subterranean termite (Isoptera: Rhinotermitidae). *Sociobiology* 13: 145–151.
- Su, N.-Y., and J. P. La Fage. 1999. Forager proportions and caste compositions of colonies of the Formosan subterranean termite (Isoptera: Rhinotermitidae) restricted to cypress trees in the Clacasio River, Lake Charles, Louisiana. *Sociobiology* 33: 185–193.
- Turchin, P. 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology* 72: 1253–1266.

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