

Research Article

***Coptotermes formosanus* and *Coptotermes gestroi* (Blattodea: Rhinotermitidae) Exhibit Quantitatively Different Tunneling Patterns**

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Tunneling behavior and the spatial dispersion of tunnels constructed by the subterranean termites *Coptotermes formosanus* Shiraki and *Coptotermes gestroi* (Wasmann) (formerly known as *C. vastator* Light) (Blattodea: Rhinotermitidae) were examined in foraging arenas. The results indicated that these two termite species construct quantitatively different tunnel systems, supporting visual observations made in earlier studies. *Coptotermes gestroi* constructed thin, highly branched tunnels, while *C. formosanus* tended to construct wider and less branched tunnels. Tunnels of *C. gestroi* showed more spatial dispersion than those of *C. formosanus*, and this species constructed a larger number of tunnels compared to *C. formosanus*. The presence or absence of food (wood) within the arena did not influence the tunneling pattern of either species. Although previous observations have suggested that these two termite species exhibit different tunneling behaviors; this is the first quantification of the differences. Comparative studies of the foraging behavior of subterranean termite species contribute to our understanding of their distribution and ecology and may help to improve pest management programs, particularly those based on placement of toxic baits. Moreover, differences in tunneling patterns may reflect different foraging strategies optimized for either tropical (*C. gestroi*) or subtropical/temperate (*C. formosanus*) environments.

1. Introduction

Subterranean termites (Family Rhinotermitidae) create ramified tunnel systems above or beneath the soil to locate their cellulosic food [1]. Sometimes these tunnels, which range from tens to hundreds meters in length, connect multiple feeding sites [2]. The morphology and architecture of termite tunnels are highly diverse, with the spatial distribution, tunnel length, width, and volume differing according to the species [3]. Lee et al. [4] observed that the tunnel geometry results from concerted work by a group of termite individuals. Campora and Grace [5] found some evidence that average worker size has an effect on group tunneling efficiency. They hypothesized that physically larger workers may have advantages in the mechanics of tunneling. Also,

tunneling behavior may be induced by both internal and external factors such as physiological, genetic, and environmental conditions [6]. Campora and Grace [7] reported that when termites were introduced into the center of a two-dimensional foraging arena filled with sand, tunnels were uniformly distributed around the perimeter of the initiation site. Su et al. [8] observed that none of these tunnels looped back towards the origin. It is difficult to identify which specific factor is responsible for observed tunnel characteristics, since tunneling behavior is the outcome of complex interactions among multiple physiological functions [6]. For example, Arab et al. [9] reported that termite trail pheromones elicit both orientation and recruitment behaviors.

The relationships among observed tunneling behaviors and external (environmental) factors are easier to study since

these factors can be more objectively defined [6]. Houseman and Gold [1] observed that tunneling rates increased in response to the concentration of sand in the soil. Su and Puche [10] and Green et al. [11] found that soil moisture positively affected tunneling rates; and Arab and Costa-Leonardo [12] reported that increased temperature increased tunneling rates. Cornelius and Osbrink [13] concluded that physical properties of soil affected both tunneling through the soil and above-ground construction of shelter tubes (protected runways between the soil and wood), and that termites tunnel through sand faster than through top soil or clay.

The tunneling behavior of subterranean termites is difficult to study in the field due to their cryptic habitats [14]. As a result, detailed analyses of foraging and tunneling behavior are largely limited to laboratory bioassays. Those experiments may help to illuminate the consequences of tunneling behavior for termite foraging strategies, and the link between the individual and population levels in tunneling dynamics [15].

In a previous study, Grace et al. [16] observed differences in the tunneling patterns of the two subterranean termites found in Hawaii, *Coptotermes formosanus* Shiraki and *Coptotermes gestroi* (Wasmann). *Coptotermes gestroi* was formally known as *Coptotermes vastator* Light in the Pacific region, until synonymized by Yeap et al. [17], and Hawaii is one of the few places in the world where *C. gestroi* and *C. formosanus* cooccur [18–20]. *Coptotermes gestroi* appeared to construct thin and highly branched tunnels, while tunnels of *C. formosanus* were wider and less branched. However, these visual observations were made in the course of feeding experiments, and the bioassay design did not permit any quantification or analyses of these apparent differences. In a comparative study of feeding and tunneling activity with Malaysian termites, Yeoh and Lee [21] depicted tunnel patterns for *C. gestroi* similar to those reported by Grace et al. [16], but did not include *C. formosanus* nor analyze the patterns. *Coptotermes gestroi* primarily occurs in the equatorial zone, while *C. formosanus* is subtropical in distribution, and Grace et al. [16] suggested that the apparent differences in tunneling might reflect different foraging strategies on the part of these two termite species optimized to fit the distribution of cellulosic resources in their respective environments.

Visual observations alone of biological or behavioral phenomena, without analysis, are of limited value in testing hypotheses. Thus, the present study was initiated in order to quantify these apparent differences, using two-dimensional foraging arenas (Figure 1) already proven useful for analysis of *C. formosanus* tunneling behavior. *Coptotermes gestroi* currently has a very limited distribution in Hawaii, and were limited to a single-field collection site for this species. However, we compensated for this very limited colony replication (atypical of termite behavioral studies) with appropriate statistical analyses. To mimic the situations normally encountered by tunneling termites, we also included arenas with two different susceptible woods as well as arenas with no wood present in the study, in order to determine if these different conditions resulted in different tunnel patterns.

2. Materials and Methods

2.1. Foraging Arenas. We used six test arenas (three for *C. formosanus* and three for *C. gestroi*) with each arena consisting of two sheets of transparent acrylic, separated by a third sheet with the interior cut out to form a 10 cm rim around the perimeter as described by Campora and Grace [7]. The upper sheet was $85 \times 85 \times 0.25$ cm and the lower $85 \times 85 \times 0.50$ cm; the two sheets were fixed together by peripheral fastening screws through the 10×0.25 cm rim in order to form an inner experimental space of dimensions $75 \times 75 \times 0.25$ cm (Figure 1). Eight small square spacers were distributed on the upper surface of the lower sheet to maintain a uniform separation of the upper and lower sheets, and the space between them filled with ca. 8 kg silica sand (40–100 mesh, 150–425 μ m sieve, Fisher Scientific, Fair Lawn, NJ) and moistened with deionized water to approx. 18% water content by weight [5]. To present an array of baits, 16 holes were drilled in four rows across the upper sheet (3.1 cm diameter, 20 cm separation, see Figure 1), each able to accommodate a plastic snap-cap vial (48 mL capacity) from which the bottom had been removed. For baited treatments, a preweighed wooden block (Douglas Fir, *Pseudotsuga menziesii*, and Southern Yellow Pine, *Pinus* spp., separate arenas for each wood) was placed in each. At the center of the upper sheet, a larger hole of 8.2 cm was drilled to accommodate a capped plastic jar of 500 mL capacity, again with the bottom removed: this served as the termite release chamber and contained two wet filter papers to provide food and moisture for the termites at the outset of the experiment. During filling, the sand was spread manually across the arena before closure, allowing no sand-free spaces to be formed under the upper sheet [23]. Finally, all arenas were stood on a metal grid supported by four glass jars and kept in a dark room. Three fluorescent lights were spaced evenly under each arena for observation of the developing tunnelling patterns.

2.2. Termites and Bioassay Procedures. *Coptotermes formosanus* individuals were collected from a field site on the Manoa campus of the University of Hawaii, adjacent to Miller Hall ($21^{\circ}17'N$; $157^{\circ}99'W$; 23.1 m above sea level) (Figure 2). *Coptotermes gestroi* individuals were collected from a field site on the west side of Oahu, approximately 40 k from the campus (Barber's Point riding stables, Kalaeloa; $21^{\circ}19'N$; $158^{\circ}02'W$; 9 m above sea level) (Figure 3).

Termites were collected from each site in wood placed beneath plastic buckets on the soil surface and were brought to the laboratory. They were removed from the wood and counted using techniques modified from those of Tamashiro et al. [24], Su and La Fage [25], and Grace et al. [26]. Approx. 1500 termites comprising 90% workers and 10% soldiers were introduced into each arena via the release chamber.

Six arenas were employed simultaneously, with three allocated to each termite species, one of each set of three allocated to each type of timber (Douglas Fir or Southern Yellow Pine) and one of the three containing no wood and designated as a nonfeeding control. The arenas were arrayed in a rectangular fashion (2×3) in a dark room lit only by

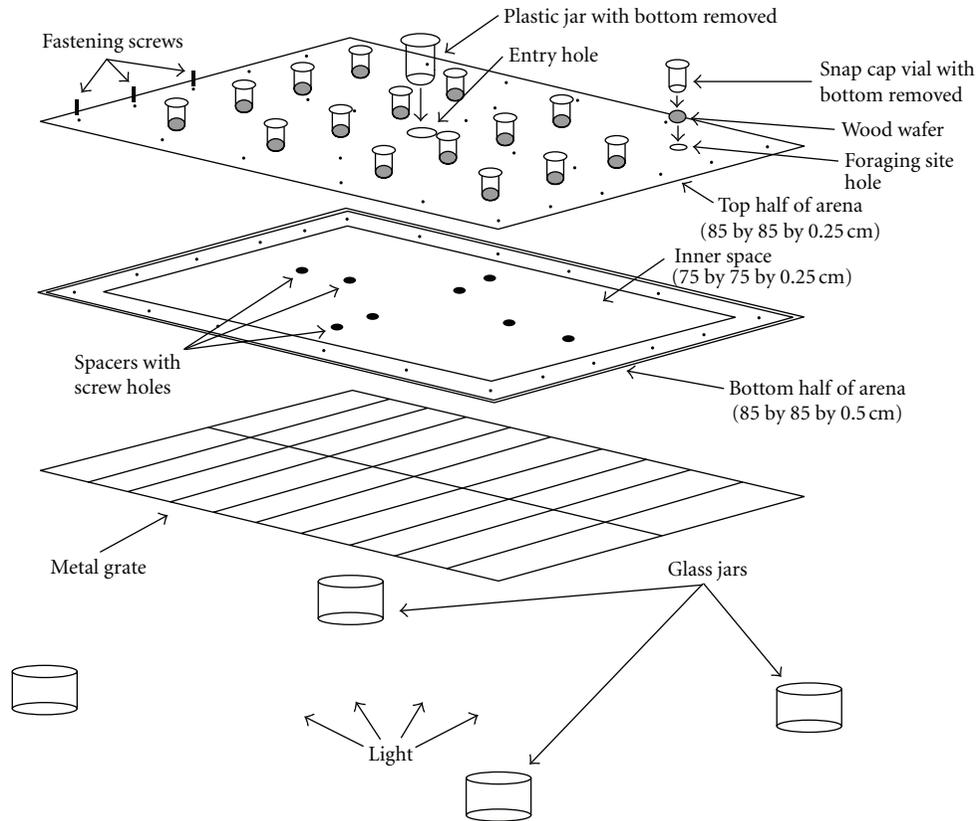


FIGURE 1: Schematic drawing of a subterranean termite foraging arena, after Campora and Grace [22]. Inner space between top and bottom halves of the arena is filled with moist silica sand.



FIGURE 2: *Coptotermes gestroi* field site at Kalaeloa, Oahu, Hawaii.



FIGURE 3: *Coptotermes formosanus* field site near Miller Hall, University of Hawaii at Manoa, Oahu, Hawaii.

the lights beneath each arena and were allocated randomly to each species and wood treatment.

Arenas were observed daily over 22 days. Temperature and humidity were recorded each day using an indoor data logger (HOBO U10 Temp/RH Data Logger). For the first five days, observations and photographs were made every six hours. From the sixth to 22nd day, observations were made every 12 hours. To monitor tunnel construction, digital photographs were taken using a Nikon D40 digital camera.

2.3. Data Analyses. Digital images of the arenas were analyzed using Adobe Acrobat Professional 8 software [27]. The parameters of interest were length of tunnels (primary, secondary, tertiary, quaternary, and other), width of tunnels (mean width), and angles formed between the primary and secondary tunnels of the two species. Tunnels were classified as primary if they originated from the release site, secondary if they branched from a primary tunnel or originated at a feeding portal intercepted by a primary tunnel, and tertiary

if they branched from a secondary tunnel or originated at a feeding portal intercepted by a secondary tunnel [7].

These parameters were used to calculate the following variables for each arena: total distance (TD: sum of all tunnel lengths in each arena), area occupied (A: TD \times mean tunnel width), numerical density within the tunnel (D : number of termites released/A), and mean speed of tunnel growth (S : TD/time) [28].

Statistical analyses were carried out using Minitab 15 software [29]. Analysis of variance (ANOVA) was used to test for significant differences in the total tunnel length (L), total mean width of tunnels (W), mean speed of tunnel construction (S), area occupied (A), and numerical density (D). ANOVA was also used to test for differences between species and the effect of presence of wood in the experiment. Tukey HSD assessed differences between colonies in pairwise comparisons. A t -test (two sample test) was used to compare results between arenas without wood and with wood. To compare different parameters measured in tunnel construction trials with *C. gestroi* and *C. formosanus*, the data were grouped as discussed below.

3. Results

After placement in each release chamber (central jar), the termites remained largely clustered in the central jar for a few hours (1–6), while some termites of both species started to move outward into the arenas. For the first six to seven days, most of the termites in all arenas were very active and made tunnels over ca. 75% of each arena. They appeared to engage in several activities throughout the test period: moving back and forth within tunnels, actively excavating sand during tunnel formation, and gathering in either small (20–40) or large groups (more than 100) at apparently random locations. From days 7–22, some wood blocks were encountered (relatively very few), and fed upon and in some cases covered with silica sand. As previously noted with *C. formosanus* [7], empty bait ports in the arenas without wood were also intercepted by termite tunnels. Arenas with *C. gestroi* showed a low rate of food location (1–4 wood blocks out of 16) and a low feeding rate (by visual estimation). However, *C. formosanus* demonstrated a relatively high rate of wood block location (3–10 blocks out of 16) and a higher feeding rate. During the last few days of the test, termite activity was low, with many termites dead and living termites gathered in groups.

Tunnel network systems differed between the two species. As previously noted by Grace et al. [16], *C. gestroi* constructed a large number of highly branched, narrow tunnels, while *C. formosanus* made fewer, wider, and less branched tunnels (Figures 4 and 5, Table 1).

There were some differences in the parameters measured in tunnel construction between the two species (Table 2). *Coptotermes gestroi* built longer ($F = 3.85$, $df = 5$, $P = 0.012$) and narrower ($F = 10.62$, $df = 5$, $P = 0.031$) tunnels, at a faster rate ($F = 3.84$, $df = 5$, $P = 0.012$), and occupied a smaller total area ($F = 27.30$, $df = 5$, $P = 0.006$) than *C. formosanus*. The lowest termite mortality was recorded in the sixth arena with *C. formosanus*, and the highest

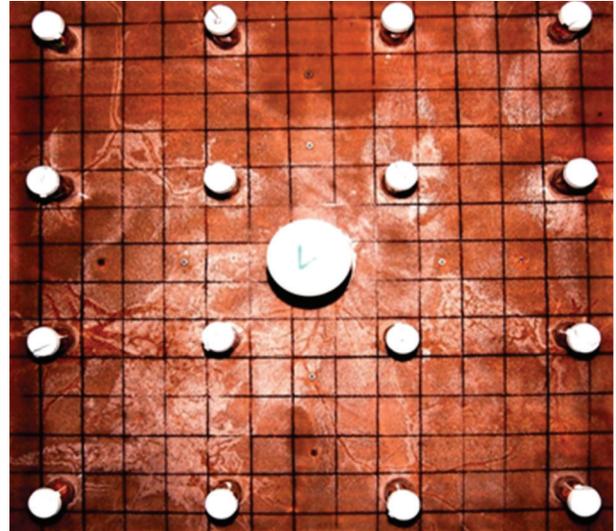


FIGURE 4: *Coptotermes formosanus* tunnels in foraging arena.

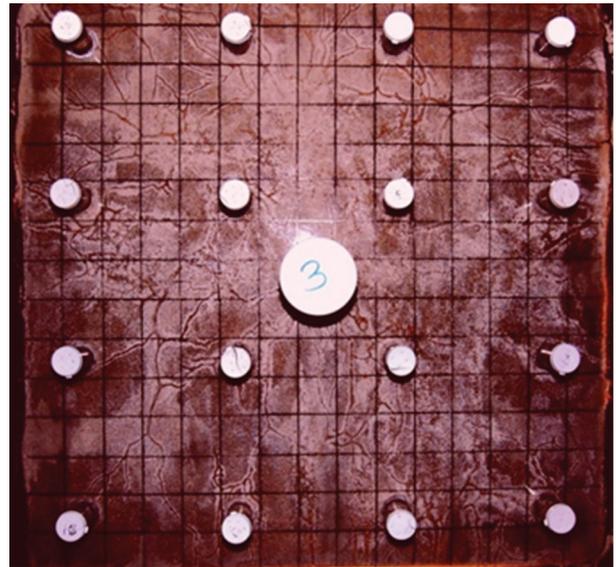


FIGURE 5: *Coptotermes gestroi* tunnels in foraging arena.

mortality was also recorded with *C. formosanus* in the fourth arena. Mean mortality values were high for both termite species, indicating that the prolonged laboratory exposure was stressful to the termites. In addition, differences in tunnel density and angles between primary and secondary tunnels were also noted, as indicated in Table 2.

There were no differences in the number of tunnels in arenas with and without susceptible wood with either termite species (Table 1 and Figure 6). Thus, tunneling patterns for the two species could be directly compared without the confounding variable of food source.

4. Discussion

The results of this study indicate that *C. gestroi* and *C. formosanus* construct quantitatively different tunnel systems,

TABLE 1: Number of tunnels in each foraging arena (C: control arenas without wood; CG: *Coptotermes gestroi*, CF: *Coptotermes formosanus*).

Arena no.	Species	Primary	Secondary	Tertiary	Quaternary	Other	Total
1	CG	5	17	23	18	10	73
2	CG	12	13	28	6	16	75
3 (C)	CG	11	18	28	11	28	96
4	CF	7	14	12	16	10	59
5 (C)	CF	4	7	7	10	11	39
6	CF	3	7	10	7	4	31

TABLE 2: Comparison of parameters measured in tunnel construction with *C. formosanus* (CF) and *C. gestroi* (CG). (TD: total length of tunnels constructed; *W*: mean width of tunnels; *A*: area occupied; *D*: numerical density within tunnels; *S*: speed of tunnel growth; *p*: primary tunnels; *s*: secondary tunnels; *wo*: workers; *so*: soldiers).

Arena No	Species	TD (cm)	<i>W</i> (cm)	<i>A</i> (cm ²)	<i>D</i> (no/cm ²)	<i>S</i> (cm/days)	Angles- <i>p</i> and <i>s</i>	Survival No. <i>wo</i> : <i>so</i>	Mortality %
1	CG	1043.56	0.08	87.66	15.40	47.43	52.13	663:20	54.47
2	CG	715.85	0.07	50.83	26.56	32.53	53.21	913:29	37.2
3 (C)	CG	1294.45	0.06	81.55	16.55	58.84	54.22	924:36	36
4	CF	706.87	0.20	166.64	8.10	37.13	38.81	485:35	65.33
5 (C)	CF	611.37	0.35	212.76	6.35	27.78	38.55	658:66	51.73
6	CF	496.0	0.50	247.01	5.47	22.55	41.10	1040:133	21.8
<i>P</i> value		0.012	0.031	0.006	0.024	0.012			0.805

(C: Controls without wood, Termite species comparison by ANOVA and Tukey, $P < 0.05$).

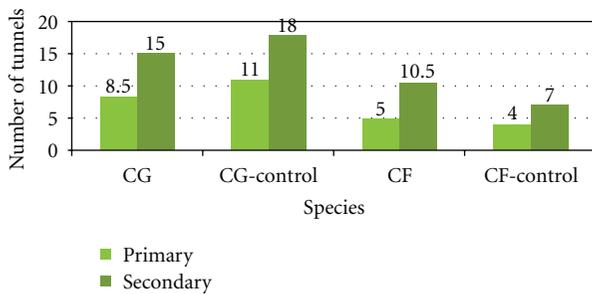


FIGURE 6: Number of primary and secondary tunnels in foraging arenas with (Douglas Fir and Southern Yellow Pine) and without (controls) food present. CG: *C. gestroi*; CF: *C. formosanus*. Within each species, tunnel numbers with and without food present were not significantly different (t -test: $P = 0.118$).

substantiating the qualitative visual observations of Grace et al. [16]. *Coptotermes gestroi* makes a large number of narrow tunnels with many branches, whereas *C. formosanus* makes a smaller number of wider and less-branched tunnels (Tables 1 and 2). *Coptotermes formosanus* occupies a larger tunneling area than *C. gestroi* and thus may locate a greater number of individual wood resources. These results support the hypothesis suggested by Grace et al. [16] that *C. gestroi* employs a foraging strategy of intensive local search, while *C. formosanus* constructs a network of longer exploratory tunnels extending over a greater area in order to locate more spatially disparate resources. Grace et al. [16] also suggested that these differences in tunneling behavior may reflect differences in the spatial distribution of cellulosic resources

in the tropical (*C. gestroi*) and subtropical (*C. formosanus*) environments favored by each of these termite species.

Although not addressed in the current study, the interaction between the trail pheromone of termite species and their food search patterns might lead to more efficient location of food [12]. Trail pheromone plays a fundamental role in the orientation and recruitment of termites [30]. Minimizing the energy used in search tunnel formation would certainly be advantageous to a termite colony. An efficient search system should optimize total tunnel length and mean tunnel length within a given search area, resulting in fairly direct foraging routes to food sources [3]. Although *C. formosanus* appeared to be more energy efficient by constructing a few, wider tunnels compared to the network of small, branched tunnels created by *C. gestroi*, the relative efficiency of these tunnel patterns in food location and accumulation would depend upon the distribution of resources in the surrounding environment.

We also examined whether different tunneling patterns resulted when there was no wood to locate within the arena. However, there were no statistically significant differences in tunnel numbers with or without the presence of wood. Campora and Grace [7] also found that the presence or absence of wood did not affect the basic tunneling pattern of *C. formosanus*. In additional work, we intend to examine whether the different tunnel patterns of these two species result in more or less rapid food discovery when resources are clumped, as might be found more often in the subtropical regions home to *C. formosanus*. Grace et al. [16] suggested that tunneling patterns may reflect such regional variation in the distribution of woody resources.

We conclude that tunneling patterns, rates, the numbers of individual tunnels produced by *C. formosanus* differ from those of *C. gestroi*. The presence or absence of wood did not influence each species' innate tunneling patterns. Based upon the results of this study, we are currently designing a foraging arena appropriate to test the hypothesis of Grace et al. [16] that the different tunneling patterns of *C. gestroi* and *C. formosanus* may reflect regional variation in the distribution of woody resources upon which these termites depend. The highly branched network of tunnels characteristic of the equatorial *C. gestroi* would appear more efficient for locating more uniformly distributed cellulosic resources, while the longer and unbranched tunnels of *C. formosanus* would provide a more efficient route to the widely separated woody resources found in subtropical or temperate environments. Thus, in a foraging arena containing widely separated (clumped) wood, one would expect that *C. formosanus* would locate these resources more quickly than *C. gestroi*. Whether or not this is the case remains to be seen, but correlation between observable termite behaviors, such as tunneling patterns, and particular characteristics of the species' environments would provide a useful tool for studying the ecology of these cryptic insects, and for understanding the current and future distributions of invasive termite species.

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