

**Comparison of Tunneling in the Laboratory and Field by the
Formosan Subterranean Termite, *Coptotermes formosanus*
(Isoptera: Rhinotermitidae)**

by

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ABSTRACT

Differences in tunneling between small groups of Formosan subterranean termite, *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae) foragers in the laboratory and foragers in the field environment were investigated. Groups from two different colonies showed no differences in amount of tunneling and wood consumption under controlled laboratory conditions; however, significant differences in tunneling and feeding were found when comparing the same two colonies in the field. Possible reasons for variation in tunneling rate between field colonies are discussed. Population estimates suggested that colony size could be a factor. Observations on tunneling in the field over a three-day period indicated that tunneling rate may also be related to air temperature, with a lag effect.

INTRODUCTION

Various aspects of tunneling by subterranean termites (Isoptera: Rhinotermitidae) have been studied in the laboratory using two-dimensional arenas and foragers from laboratory colonies (Reinhard *et al.* 1997, Robson *et al.* 1995, Pitts-Singer & Forschler 2000, Hedlund & Henderson 1999) or discrete groups of foragers extracted from field colonies (Su & Puche 2003, Puche & Su 2001a, Puche & Su 2001b, Puche & Su 2001c, Tucker *et al.* 2004, Cornelius & Osbrink 2001), but there is little information on tunneling by foragers that are a functional part of a large field colony (Evans 2003). Even though many of the authors of the works referenced above

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recommend caution in interpreting their results due to the discrepancies of scale and the number of foragers used, utilizing small numbers of foragers in a small space can lead to a certain amount of criticism (Evans 2003). This presents a problem since the increased popularity of baits and non-repellent termite control treatments has meant that understanding subterranean termite foraging behavior is necessary for termite control, and the use of artificial arenas is one of the most practical means to uncover their hidden tunneling behavior as they search for food.

Puche & Su (2001b) approached this dilemma with fractal analysis and found that fractal geometry could be an effective method to analyze tunneling systems independent of scale. Using this method with artificial arenas they found that tunnel abundance, or the area of space explored, did not significantly increase past a certain threshold number of foragers. This was determined to be approximately 1,000 termites/arena. In addition, they demonstrated that tunnel complexity remained unchanged between foraging groups ranging from 250 termites to 2000 termites (Puche & Su 2001c). Evans (2003) addressed the issue by using foragers from an actual colony of *Coptotermes frenchi* Hill, rather than groups of isolated foragers. However, the colony he used was confined to a 50 gal. drum and therefore was not completely representative of a field colony that is actively searching for food within a large underground foraging network.

Our objective in the present study was to investigate whether differences exist in tunneling between small groups of termite foragers in the laboratory and foragers in the field environment. We set up two-dimensional foraging arenas in the laboratory, and in similar arenas in the field directly over active foraging sites of two colonies of the Formosan subterranean termite, *Coptotermes formosanus* Shiraki. Observations were made of daily tunneling, and the amount of wood consumed was analyzed. In addition, we closely monitored tunneling in the field over a three-day period to determine if tunneling activity followed a circadian rhythm.

MATERIALS AND METHODS

Arena Design

Arenas used in the laboratory (Fig. 1B) were identical to those used by Campora & Grace (2001) in previous tunneling research, with foraging

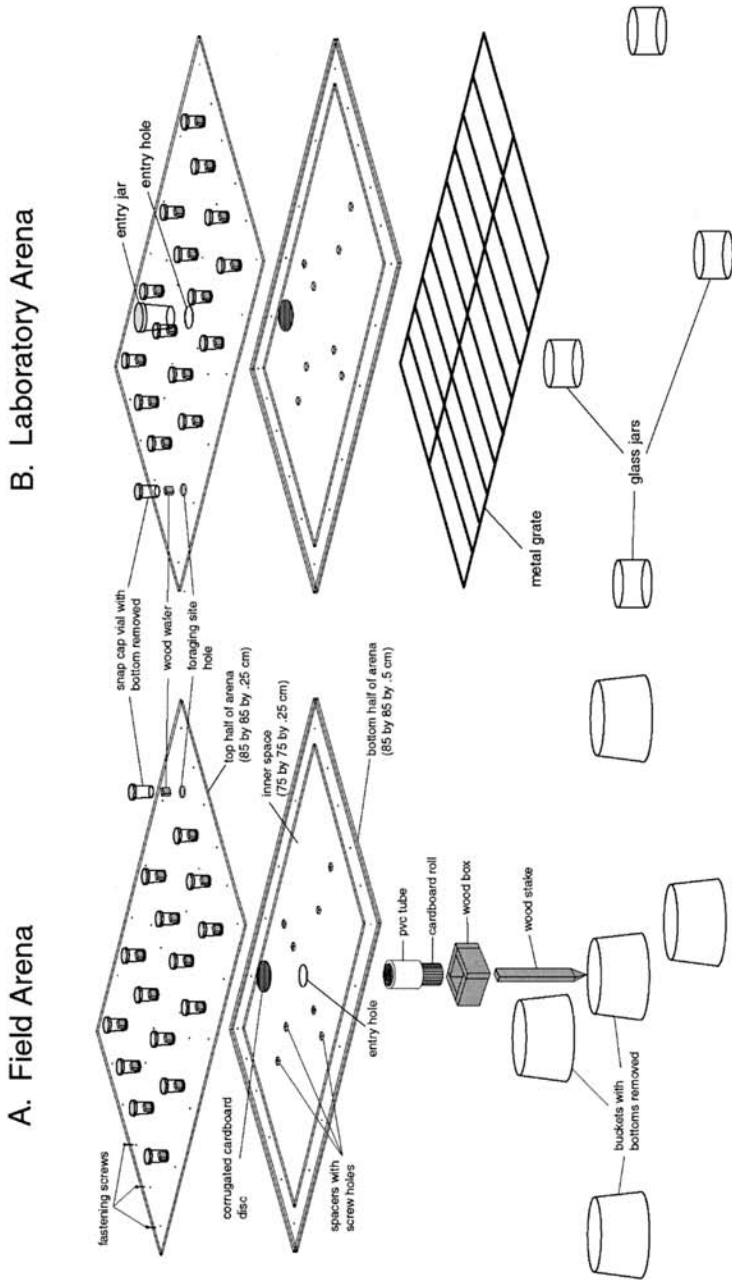


Fig. 1. Termite foraging arena design and set-up in the field (A) and laboratory (B).

sites containing pre-weighed wafers of Douglas fir, *Psuedotsuga menziessii* (Mirb.) Franco. Arenas implemented in the field were constructed using the same materials as the laboratory arenas, but were slightly modified in design (Fig 1A). The field design was altered such that when installed over an active Formosan subterranean termite foraging site, termites entered the arena from a hole in the center in the bottom of the arena rather than the top. To seal the bottom, a corrugated cardboard disc was affixed directly over the entry hole with an adhesive. To minimize variation between the two arena types, identical cardboard discs were added in the same manner directly under the entry hole in laboratory arenas. The active foraging sites in the field were previously maintained with Douglas fir box traps, using a modified version of the protocol described by Tamashiro *et al.* (1973). Before installation of the arenas, the box traps were removed and a new Douglas fir stake was driven into the soil approximately to ground level. A much smaller box constructed of Douglas fir lumber (10.8 by 8.6 cm) was then placed over the stake. Corrugated cardboard, tightly rolled to the same diameter as the arena entry hole, was inserted into the box so that the bottom was flush with the bottom of the box and the top extended out 9.5 cm. The top section of the cardboard roll was covered by PVC pipe so that only 7.0 mm of the tip protruded. A plastic bucket with the bottom removed was placed over the box/cardboard/PVC assemblage (Fig 1A). The arena was then mounted such that it rested on the rim of the bucket and PVC pipe, with the protruding tip of the cardboard roll inserted into the arena entry hole such that its surface was flat against the cardboard disc. Four additional buckets were placed at the corners of the arena to provide support. Once installed the entire apparatus was covered by a plywood box (1.25 by 1.25 m).

Protocol

Three arenas were installed over active foraging sites in each of two territories occupied by separate *C. formosanus* colonies, colony A and colony B. Colony A was located at the University of Hawaii agricultural experiment station in Waimanalo, and colony B was located on the Manoa campus of the University of Hawaii. Three separate arenas for each colony were also set up in the laboratory with groups of 1,500 termites (10% soldiers) added to each. Termites for laboratory use were extracted from collected

box traps, counted, and added to arenas on the same day. Termites in both the field and laboratory arenas were allowed to tunnel for a period of 7 days. In contrast to the laboratory arenas, which were permanently backlit, field arenas were backlit with fluorescent lighting only during the photographs. Digital photographs of tunnel galleries were taken each night (Coolpix 995 digital camera, Nikon, Melville, NY). During one 72 h period, tunneling was monitored at three-hour intervals for two field arenas within one colony to examine temporal fluctuations in tunneling rate. During daylight hours of this three-hour photographing frequency, the plywood arena housings were first covered with 5 mm black plastic sheeting to maintain a dark environment. In the absence of sunlight, the housing lids were then removed and the arenas were photographed.

Air temperature immediately outside laboratory and field arenas was recorded during all tunneling trials with HOBO H8 Pro Series data loggers (Onset Computer Corporation, Bourne, MA). Laboratory arenas were not in a temperature-controlled facility and were subject to heat fluctuations related to the outdoor environment. Tunneling trials were conducted on different dates over a period from June 8 to October 30, 2001 (colony A field: June 8 - July 17; colony A lab: August 29 - September 9; colony B field: September 15 - October 5; and colony B lab: October 23 - October 30). At the end of every field and laboratory trial, wafers were removed from the foraging sites of each arena and weighed to determine wood loss. Population estimates were obtained upon completion of all tunneling trials for both colonies using a triple mark-release-recapture method (Begon 1979).

Analysis

Tunnel surface area was calculated from images using ArcView 3.2 GIS software (ESRI, Redlands, CA), and search patterns were compared between field and lab arenas. Analysis of variance using the MIXED procedure (SAS Institute 2001) was used to determine effects of colony and treatment (arena type) on total area tunneled and feeding.

RESULTS

We did not quantify tunnel pattern or complexity, but there were no obvious differences in the general pattern of resource discovery between termites

in the laboratory and the field. Tunneling in both field and laboratory arenas followed a similar pattern with tunnels emanating out from discovered sites, then intercepting nearby sites and radiating out again in sequential fashion (Fig. 2). This pattern sequence was consistent with previous laboratory arena studies (Campora & Grace 2001), except tunnels entering the arena were not

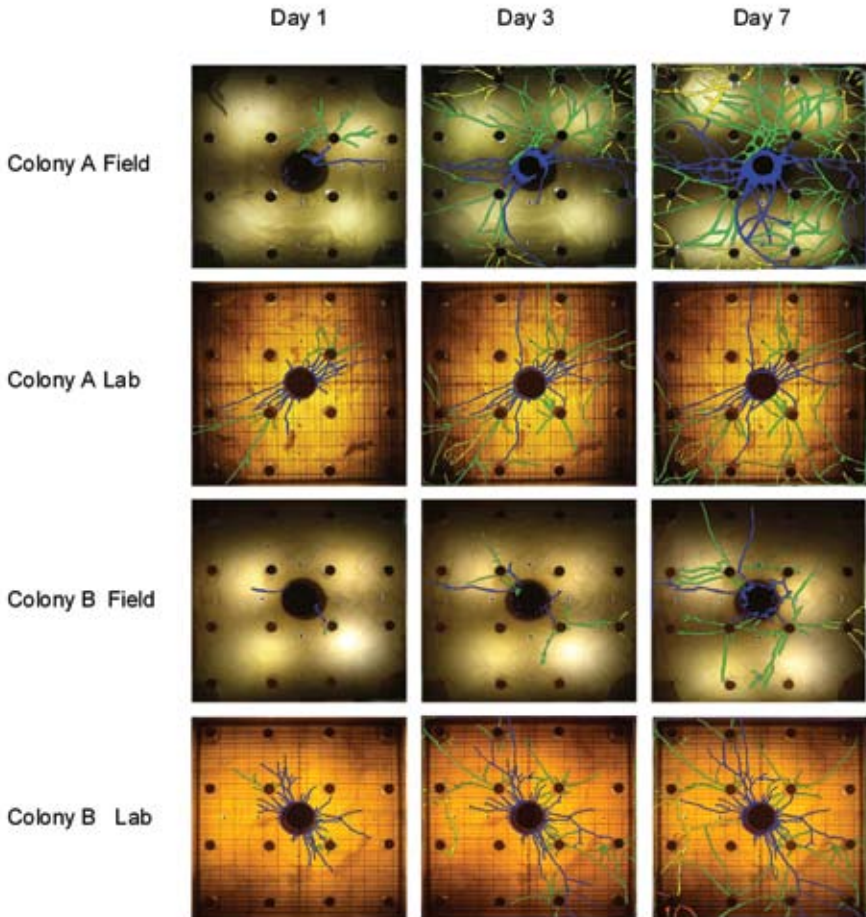


Fig. 2. Images of field and laboratory arenas with digitized tunnels showing the sequence of gallery formation representative of both termite colonies. Tunnels shown in blue are primary tunnels originating from the center. Secondary tunnels (green) originate from sites discovered by primary tunnels. Tertiary tunnels (yellow) originate from sites discovered by secondary tunnels. Quaternary tunnels (orange) originate from sites discovered by tertiary tunnels.

randomly distributed. This was due to the corrugated cardboard discs located at the termites' entry point into the arenas. Tunnels entering arenas in both the laboratory and field portions of this study continued outward with the same orientation as the corrugations of the center cardboard disc. Although tunneling patterns were similar in both the field and laboratory, there was a significant colony by treatment effect on total area tunneled ($F = 107.42$; $df = 8$; $P < 0.0001$) (Fig. 3) and on the amount of wood consumed ($F = 151.75$; $df = 8$; $P < 0.0001$) (Fig. 4). Temperature varied among foraging trials with the largest difference between the two laboratory tests (Fig. 5). Over the 72 h period for which we collected data every three hours, tunneling rate in the two arenas was erratic but appeared to be related to temperature with a lag effect (see Fig. 6). Population estimates for colonies A and B were $3,184,286 \pm 469,675$ and $2,072,475 \pm 105,077$ respectively.

DISCUSSION

Our results indicate that tunnel patterns of the Formosan subterranean termite are the same when observed in the field or laboratory. The only

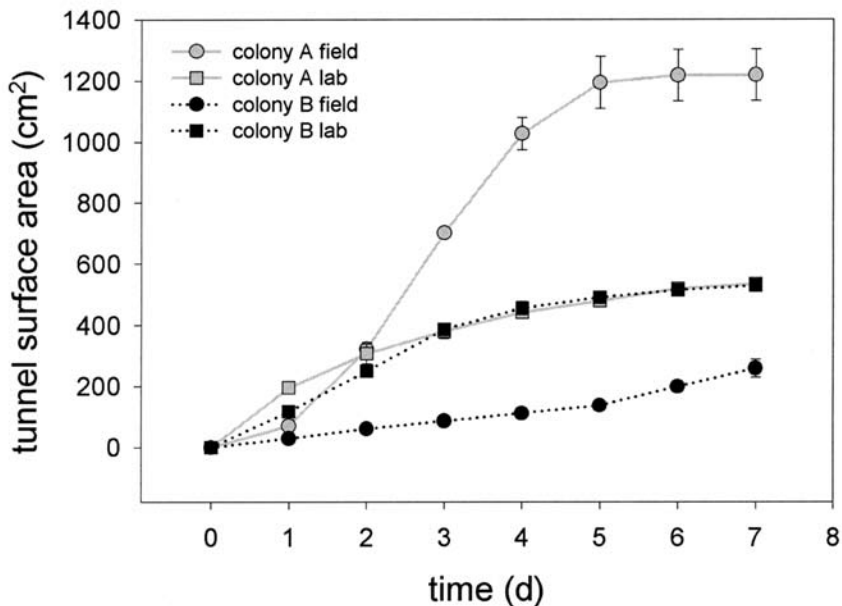


Fig. 3. Mean cumulative tunneling by termite colonies in the field and laboratory.

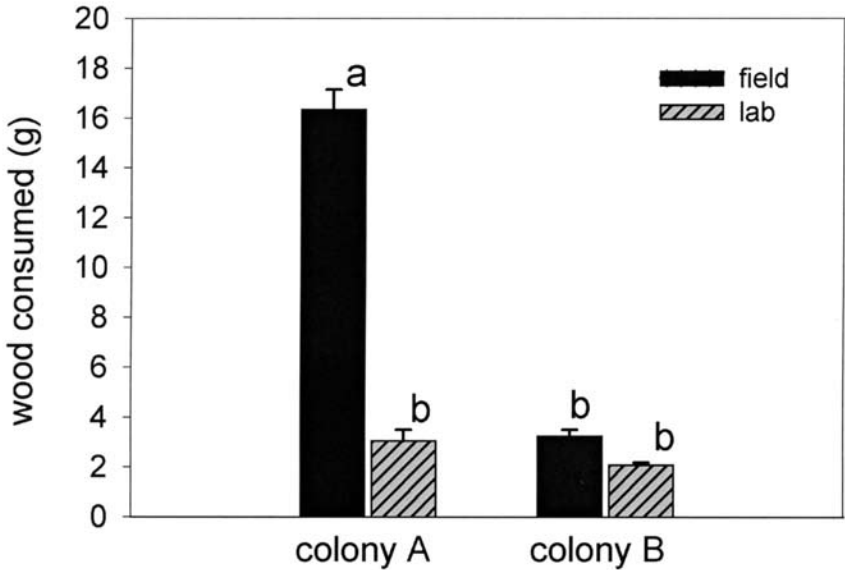


Fig. 4. Mean wood consumption by termite colonies in the field and laboratory. Means with the same letter are not significantly different.

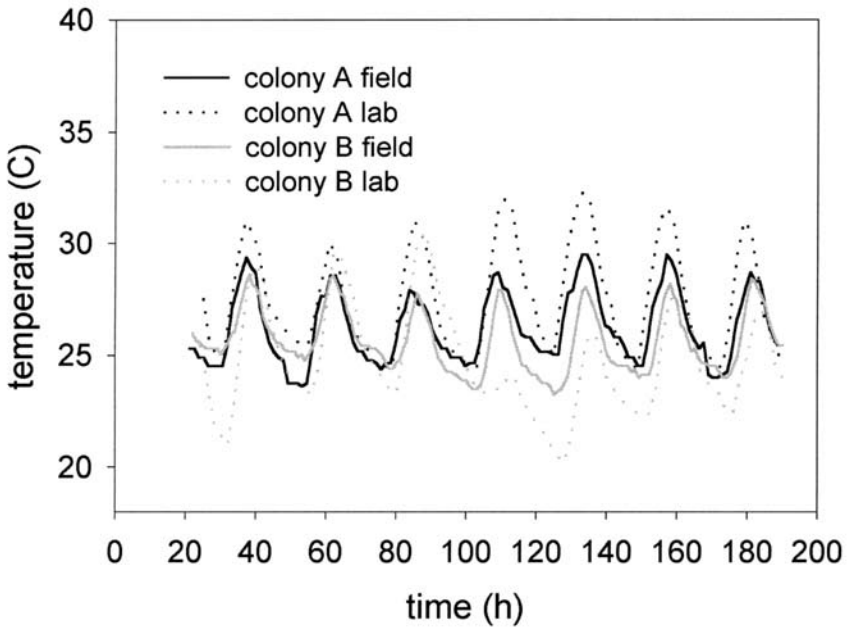


Fig. 5. Temperatures recorded during laboratory and field tunneling trials.

exception was that initial direction of tunnels entering the arena was not random, and was oriented in the direction of the corrugations of the center cardboard disc. This presented further evidence that subterranean termites not only utilize guides when tunneling (Pitts-Singer & Forschler 2000), but that they may continue tunneling in the general direction that guides are oriented even though the guide may have ended.

We also demonstrated that differences in rate of tunneling can exist between colonies in the field. There are a variety of factors that can influence a colony's foraging behavior in the field. Two of the most important factors may be temperature and moisture (Haverty *et al.* 1974). Temperature is somewhat confounded in this study due to the fact that tunneling trials were conducted on different dates in settings where the temperature was uncontrolled and fluctuated with the outside environment. Temperatures recorded during each of the trials, however, were not substantially different. In fact the greatest difference in temperature occurred between the two laboratory trials, and in these trials there were no significant differences in area tunneled.

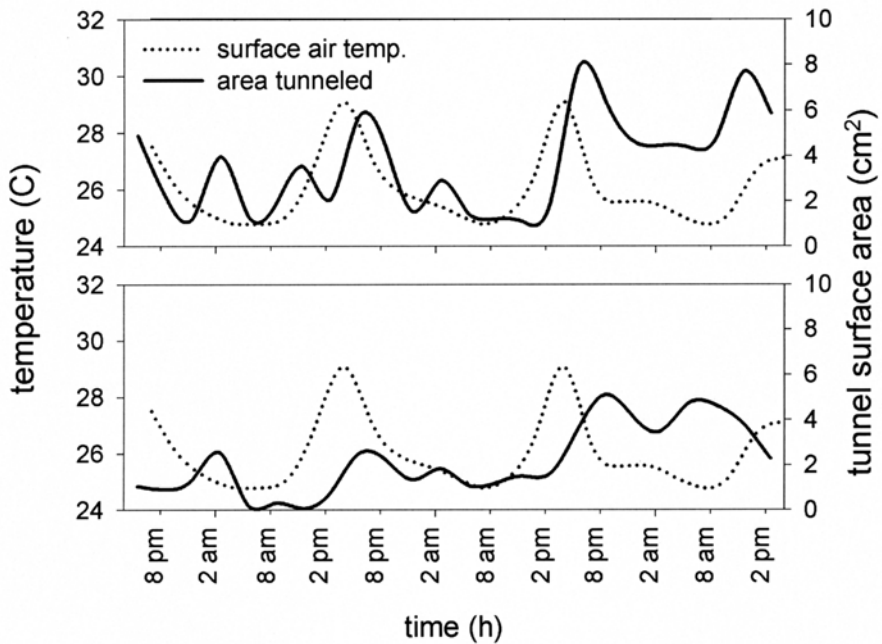


Fig. 6. Comparison of tunneling activity and temperature of two field arenas over a three day period.

Moisture, on the other hand, was present in equal amounts in all arenas, therefore, if tunneling in the arenas was affected by water, the differences in tunneling rate must have been related to differences in water needs between the colonies. Puche and Su (2001a) provided evidence that in the laboratory, tunneling foragers are attracted to soil moisture gradients. If colony B was located in an area without water readily available, this could explain its much stronger tunneling response when entering the moist sand of the arenas. The two field locations in this study were similar with regard to precipitation, but we can only speculate on the amount of water that was actually available to the two colonies. Haagsma & Rust (1995) suggested that when compared to undisturbed environments, urban environments are more stable with respect to abiotic factors such as soil moisture. Under this assumption, colony B, being situated in an urban setting, could have possibly had more access to artificial sources of moisture. This would give the foragers from colony B no added incentive to tunnel in moist sand. It should be noted, however, that even though colony A was in a more natural setting, it was not located in a completely undisturbed environment. Because colony A was situated in an agricultural area not far from irrigated fields, it was most likely not too dissimilar from colony B with regard to water availability in the field.

Differences in foraging activity by subterranean termites due to temperature and moisture are more typically correlated to seasonal differences (LaFage *et al.* 1973, Haverty *et al.* 1975, Delaplane *et al.* 1991, Haagsma & Rust 1995). In Hawaii, these factors do not fluctuate to the extent that they do in temperate areas. Furthermore, while some seasonality does occur in Hawaii, there were no major shifts in temperature or precipitation observed during the period of time over which all the trials were conducted. The fluctuations in tunneling activity we observed throughout the day in the two arenas of Colony A did appear to be related to temperature. The apparent time lag between tunneling and air temperature may be due to the fact that foragers are responding to the soil temperature just below the air/soil interface.

It is more likely that factors responsible for the differences we observed between the two colonies in the field were related to conditions intrinsic to the colony (i.e. population size) and the biotic environment (i.e. available food resources) rather than environmental and abiotic conditions. Assuming the population estimates provided correct approximations of the colonies'

relative sizes, colony A's greater tunneling activity and wood consumption in the field were possibly reflective of a greater need for food to sustain its larger foraging population. Another explanation could lie in the location of the arenas within the two colonies' foraging territories. Research with a higher termite, *Macrotermes bellicosus* (Smeathman), has also shown that foraging pressure is not necessarily equally distributed throughout a colony's foraging territory (Traniello & Leuthold 2000). This termite spatially allocates foraging and concentrates on certain sectors of its gallery system. Similarly, feeding activity by *C. formosanus* has been shown to vary throughout feeding sites within a colony's foraging range (Grace *et al.* 1996). In the current study, the location of the arenas within the foraging territories could have determined how many foragers entered them. Perhaps by chance we placed arenas over a hot spot of colony A's territory where many workers were being allocated at that time, and we may have placed the arenas over an area of low activity in colony B's range.

There is also evidence to suggest that tunneling by a group of Formosan subterranean termites is negatively correlated to the amount of food available (Hedlund & Henderson 1999), therefore if one colony had more food resources to utilize than another, it might not be as quick to explore new areas for food. Due to the cryptic nature of subterranean termites, it is not possible in the field to determine where all of their feeding sites are, but it is possible that a primarily urban environment may provide singular food resources on a large scale, such as man-made wooden structures, that do not promote searching behavior to the same extent as a natural/agricultural environment which provides smaller scattered food items.

Our results also demonstrated that the threshold of 1,000 workers/arena established by Puche & Su (2001c) does not necessarily apply to arenas used in the field. We did not perform fractal analysis on the tunnel networks, but in terms of total tunnel area, the amount of tunneling was significantly greater in field arenas with an indefinite number of foragers compared to laboratory arenas containing 1,500 termites per arena.

In conclusion, we found that the basic pattern of tunneling by *C. formosanus* foragers is the same when observed in the field or laboratory. Furthermore, tunneling activity of *C. formosanus* foragers fluctuates throughout the day and is possibly related to temperature. Differences in daily tunneling rate can

occur between colonies of *C. formosanus* in the field that are not apparent when making comparisons using equal numbers of foragers in the laboratory. In this study the factors affecting tunneling in the field were probably those that were intrinsic to the colony such as forager population size, resource availability, and forager allocation. This variation of tunneling activity between colonies in the field provides evidence that some colonies may be more difficult to control than others when using non-repellent termiticides, particularly baits.

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