

FORAGING BEHAVIOR OF SUBTERRANEAN TERMITES (ISOPTERA: RHINOTERMITIDAE): FOOD DISCOVERY AND MOVEMENT OF TERMITES WITHIN ESTABLISHED GALLERIES

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Abstract Unlike insects foraging above ground where individuals can explore over an area and then lay a recruitment trail for others to follow, subterranean termites search for food by constructing underground tunnels. Studies have showed that termite tunnel orientations are affected by physical irregularities and moisture and olfactory gradients in soil. In the featureless soil, termite tunnels are excavating in a nonrandom pattern that evenly partitions the search area to increase the search efficiency. The overall morphology of termite tunnels showed the characteristic fractal structure, and such structure is constructed one bite of soil at a time by individual termites. Our study showed that path integration is one mechanism by which termites orient their tunnels, and that external cues are not necessary for subterranean navigation. They appear to use self-reference for orientation. While the food searching and discovery by propagation of subterranean tunnels are nonrandom, the movement of termites among "discovered" food sources within the galleries is best described by a random model according to computer simulations.

Key Words Tunnel propagation, food location, food acquisition, forager movement

INTRODUCTION

Food location is the major element in the study of foraging behavior. One unique aspect of subterranean termites is that they have to discover food in soil by constructing underground tunnels. Once the food is discovered and connected to the galleries, another important element of the foraging behavior is the food acquisition and transfer by individual termites moving within the existing tunnels that lead to multiple existing food sources. These two elements deal with vastly different behaviors of subterranean termites, and motives behind these two studies differ from each other. As with other animals, food location strategy relates to basic questions such as efficiency in energy allocation for its acquisition, but also has an applied implication for better baiting and control of subterranean termites. Study on the movement of subterranean termites within the existing galleries arose initially (Su et. al., 1984) with the need to examine if a toxicant bait placed in one portion of the vast gallery system may be visited and acquired by the majority of foraging termites. This paper reviews these two elements of foraging behavior of subterranean termites.

FOOD LOCATION

Finding food in soil is a combined effort by a group of termites that excavate tunnels. Individual termites remove one bite of soil at a time at the tip of the tunnels, yet the combined results produce a relatively predictable pattern of tunneling geometry that can be characterized by a fractal model (Puche and Su, 2001a). The coordinating procedure by which such tunneling structure is constructed by a group of termites is largely unknown, and the mechanism for tunnels to encounter food sources in soil is even more puzzling. Based on the observation of small two-dimensional foraging arenas, Robson et al. (1995) suggested that tunnel distribution of the eastern subterranean termite, *Reticulitermes flavipes* (Kollar) was optimized for food searching efficiency. Using a similar device, Hedlund and Henderson (1999) indicated that food size affected tunnel volume and length of the Formosan subterranean termite, *Coptotermes formosanus* Shiraki. Campora and Grace (2001), however, concluded that the presence of food did not impact tunnel distribution of *C. formosanus*. Puche and Su (2001b) also reported that tunneling geometry of *C. formosanus* in laboratory arenas was not affected by

the presence of food, but tunneling activity increased towards a positive moisture gradient (Su and Puche, 2003). Aside from moisture, attractants permeated from decayed wood may also alter the orientation of termite tunnels (Su, 2005).

To understand the physical characteristics of termite tunnel geometry, Su et al. (2004) reduced tunnel structure into basic component by a protocol for quantifying movement pathway. A computer simulation program incorporating the measured components was used to reconstruct termite tunnels and to identify other critical components. Ten components were identified as the minimum elements needed to re-construct plausible termite tunnel structure, including (1) the number of primary tunnels originated from the release chamber, (2) linear length (defined as the linear line connecting two closest points of a tunnel that did not deviate off the tunnel path) of primary tunnel segments, (3) turning angle of each linear segment of a primary tunnel, (4) branching angle of secondary tunnels, (5) probability of branching per each linear segment of a primary tunnel, (6) termination probability for primary tunnels, (7) termination probability for secondary tunnels, (8) the probability of continuing through an intersection when two tunnels meet, (9) the maximum deviation from the start angle, and (10) the minimum angle between two primary tunnel origins. A fractal analysis indicated that the simulation program produced tunnels with a statistically similar complexity to those produced by termites. The simulation program also provided insights into termite tunnel structure, namely the truncation of tunnels intersecting other tunnels, and the tendency for tunnels to radiate away from the origin without looping back towards the origin. The results lead us to establish some hypothesis to identify what may guide termites to construct a subterranean tunnel.

In a laboratory study (Bardunias and Su, unpublished data) we demonstrated that, in the absence of odor or moisture gradients in the soil, termites were orienting their tunnel excavation by tracking their position relative to a point of origination. Tunnel propagation does not require information from local pheromonal or stigmatic cues, nor the use of a global compass. Our next phase of this series of studies is to understand how a group of termites coordinate their efforts in excavation of tunnels.

FOOD ACQUISITION AND TRANSFER

During the early developmental stage of termite baiting technology, one aspect of termite behavior that was thought to be critical was feeding site selection by foragers among established sites (Su et al., 1984). The foraging gallery system of subterranean termites can be extensive and baits have to be applied to only a small portion of the nesting network. Because the trophallactic transfer of bait toxicant was largely unknown at the time, there was a need to determine if a toxicant could be delivered by direct feeding. Su et al. (1984) placed paper dyed with Sudan Red 7B in "bait" stations for *C. formosanus* colonies and measured the proportions of dyed foragers in "sampling" stations of the same colony, as well as their feeding frequency. During the test period, the majority of sampled termites acquired dye makers. Because Sudan Red 7B was not transferred via trophallaxis in laboratory studies (Su et al., 1983), it was concluded that all foraging termites would visit the bait stations, given sufficient time. Feeding frequency data, as measured by the dye concentration in individual termites, also suggested the absence of feeding site fidelity. Because the dye marker was used to emulate a bait toxicant when it is introduced into a colony, it was concluded that the dye (and the toxicant) could be distributed throughout the colony members given sufficient time.

Findings of Su et al. (1984) encouraged further studies of bait toxicant technologies, leading to the successful development of the first commercial bait product with the chitin synthesis inhibitor, hexaflumuron (Su, 1994). However, these results were often misinterpreted as random movement of termites that were marked and released for population estimate studies, or the random search of food in soil by subterranean termites. Foraging site selection by foragers is not equivalent to the movement of marked and released termites and should not be confused as such. As discussed the above, subterranean termites locate and reach food in soil through tunnels constructed by a group of termites, and the "random" movement of an individual termite (even if that is the case) within the established tunnels does not imply the "random" search of food. In a recent study, Su and Scherer (2003) used a computer simulation program to re-examine the feeding frequency data of Su et al. (1984), and confirmed the earlier conclusion that the lack of feeding site fidelity was the most likely explanation for the data.

The early study by Su et al. (1984) was needed because the trophallactic transfer of bait toxicant was unknown at the time. Trophallactic transfer of hexaflumuron in termites has since been documented (Sheets

et. al., 2000), and numerous studies have also demonstrated the elimination of field colonies of subterranean termites by hexaflumuron baits (Su, 2003). With these compelling data indicating that field colonies could be impacted by applying hexaflumuron baits at one portion of the vast feeding network, the need to investigate the feeding site preference of termites may no longer be relevant if the objective is to develop information for baiting technology.

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