

FOOD LOCATION AND DISCRIMINATION BY SUBTERRANEAN TERMITES (ISOPTERA: RHINOTERMITIDAE)

¹J. KENNETH GRACE AND ²CORY E. CAMPORA

¹Department of Plant and Environmental Protection Sciences, University of Hawaii at Manoa, 3050 Maile Way, Honolulu, Hawaii 96822

²Environmental Planning, Naval Facilities Engineering Command Pacific, 258 Makalapa Drive, Suite 100 Pearl Harbor, Hawaii 96860-3134

Abstract Tunnel construction by *Coptotermes formosanus* Shiraki is initially random, with tunnels radiating outward in a uniform circular distribution from the point of origin. The degree of branching of these tunnels may be species-specific, and reflect the pattern of occurrence of food resources in different environments. As open spaces, wood, or inedible objects are encountered in the soil, tunnels outward from these substrate anomalies are no longer distributed randomly. Rather, multiple exit tunnels are constructed in the same general direction as the entry tunnel. In foraging arenas, these exit tunnels never reversed direction. When an open space was encountered, the directional vector of the exit tunnels was less pronounced due to the large number of tunnels fanning outward from the open area. Termite tunneling shifts from the original uniform distribution into a more localized and directional distribution as food sources are discovered. Any environmental cues (e.g., guidelines, thermal shadows) may alter the tunnel distribution. At a very short distance, it is likely that gradients from the diffusion of both gases and plant or fungal metabolites provide directional cues. Trail pheromone is likely to play a major role in recruitment of foragers to acceptable food sources. If a single component is responsible, then gradients appear necessary to maintain this behavior, since acclimation can occur with constant continued exposure. An ephemeral recruitment component may be deposited along with a more stable orientation component. Wood treated with disodium octaborate tetrahydrate was gradually avoided over a period of several days, with termite foraging activity declining in tunnels in the vicinity of the treated wood, and increasing in portions of the arena containing untreated wood. Termite mortality did not occur in the vicinity of the treated wood, so the avoidance cannot be attributed to a necrophobic response. When the positions of borate-treated and untreated wood samples were switched in these studies, termites investigated the borate-treated samples in their new locations, followed by gradual avoidance. Termite return to the sites that had been previously occupied by borate-treated wood was very slow, and ceased immediately when borate-treated samples were again placed in these same locations. Resources appear to be mapped within the established foraging network with respect to their acceptability.

Key Words *Coptotermes formosanus*, subterranean termites, foraging, tunneling

INTRODUCTION

Foraging by subterranean termites may be divided into three phases. The first phase consists of locating a suitable food resource. This involves exploration of the substrate through the creation of tunnel networks. Colonies of subterranean termites depend upon these underground networks to access the resources necessary for their sustenance. Second, as food items are discovered, additional foragers must be recruited to begin feeding and distributing nutrients throughout the colony. This is accomplished, at least in part, through the use of trail pheromones deposited from the sternal glands of individual workers (Stuart 1969). Finally, as multiple feeding sites are established, foragers must decide where to allocate their feeding efforts, since not all food resources may be equally acceptable. The Formosan subterranean termite, *Coptotermes formosanus* Shiraki, can modify recruitment according to both the quality and quantity of a food resource (Waller and LaFage, 1987).

This foraging process is dynamic and changes over time relative to the quantity of available food resources and the feeding requirements of the colony. Food in the form of wood does not change locations, but each food item is a non-renewable resource and depletes over time. Existing food resources may also become unsuitable or even toxic to termite foragers in urban situations where insecticides and wood preservatives are used. Subterranean termite colonies must therefore continually search for new food and discriminate among existing food resources in order to ensure their growth and prolonged survival. In this paper we summarize recent research on foraging behavior as it pertains to the three phases of subterranean termite foraging described above.

FOOD LOCATION

One of the primary questions about subterranean termite search behavior is whether tunneling is random or systematic. Tunneling studies with groups of termites in artificial foraging environments suggest that it is both random and systematic, at different stages and in response to the immediate environment. Robson et al. (1995) were the first to describe non-random search geometry in subterranean termites. These researchers found that tunnel branches emanating outward from a center point were distributed to maximize the angles between them; however, they found no significant preference in the direction of the branched systems. In other words, the tunnels were non-random in relation to each other within an individual network, but the initial direction of tunneling was random.

Random directional preference in tunneling was also reported by Campora and Grace (2001). They found that in a homogeneous tunneling environment, tunnels displayed a uniform circular distribution from the center point of origin, meaning that there was no preference for any specific initial orientation. Examining the distribution of tunnels further outward from the center at a circular perimeter where physical anomalies in the tunneling substrate were present, Campora and Grace (2001) observed that the distribution of tunnels was no longer random. Tunnels were significantly clustered at locations in the outer perimeter where the substrate anomalies were present. These results suggested that objects in the soil can influence the tunneling response and that recruitment can play a role not only in feeding but also in tunnel formation.

Additional research conducted by Campora (2004) determined that certain characteristics of objects in the soil may cause a greater increase in localized tunneling activity than others. In general, when an anomaly in the substrate, such as an embedded food object, a solid non-food object, or an open space was encountered by termites, they created multiple tunnels that fanned outward in the same direction as the tunnel that originally encountered the anomaly. The resulting distributions of tunnels exiting these types of anomalies were non-random, because termites never reversed direction and constructed tunnels directly back towards the point of origin. When the number of exit tunnels from these three anomaly types (embedded wood, a solid non-food object, or an open space) was compared, it was found that termite foragers constructed significantly more tunnels from the open spaces than they did from the food and non-food objects. Furthermore, circular statistics conducted on the distributions of pooled exit tunnels for all three anomaly types revealed that the mean directional vector was weakest for the tunnel distribution around the open space, indicating that when the termites encountered a void in the substrate they tended to create exploratory tunnels outward in a wider fan.

Subterranean termites may show no directional preference for foraging in uniform soil, but an underground environment free of physical, biological, and chemical cues are most likely very rare. Recent research has demonstrated that there are many factors in addition to objects encountered in the substrate that have the potential to influence the direction of termite foraging. For example, experiments with two-dimensional foraging arenas have shown that moisture in the tunneling substrate stimulates tunneling by *Coptotermes* spp. (Su and Puche, 2003; Evans, 2003). Additionally, termites may also be attracted, at least over a short distance, to areas that contain chemical exudates from food resources. Cornelius et al. (2002) found that *C. formosanus* explored sand that was treated with methanol extracts of fungus-infected sawdust significantly more than sand treated with extracts from uninfected sawdust. Other factors such as loose soil, the presence of guides or linear objects, and existing passages or gaps have also been shown to stimulate tunneling behavior (Tucker et al., 2004; Pitts-Singer and Forschler, 2000). Thermal gradients have also been shown to promote foraging in mesic habitats for two species of desert subterranean termites (Ettershank et al., 1980).

There is also evidence of species specific tunneling patterns by subterranean termites. Differences have been described in tunnel width and complexity between species of *Reticulitermes* and *Coptotermes* (Cornelius and Osbrink, 2001; Puche and Su, 2001a; Puche and Su, 2001b), but there is also evidence of possible differences in the degree of tunnel branching between species within the same genus. Grace et al. (2004) observed striking differences in tunnel geometry between *C. formosanus* and *Coptotermes vastator* Light. Tunnels created by *C. vastator* in glass jars during feeding trials were much thinner and more highly branched than those created by *C. formosanus* during the same trial. Differences in tunnel pattern between these two species may be the result of contrasting foraging strategies that have arisen due to differences between the distribution of food resources in tropic and sub-tropic areas. Assuming that in tropical zones, plants are more ubiquitous and evenly distributed compared to sub-tropical and temperate latitudes, it is plausible that the more tropical species, *C. vastator* (Uchima and Grace, 2003), employs a more intensive local search pattern because it evolved in an environment where food resources were located close together.

RECRUITMENT TO NEW FOOD SOURCES

Deposition of trail pheromone appears to play an important role in the recruitment of foragers to feed in certain areas within a termite colony's tunnel network (Tschinkel and Close, 1973). The sternal gland is the only source of trail pheromone, and while a single active compound has been identified in the trail pheromone of both *Reticulitermes* and *Coptotermes* species (Matsumura et al., 1968; Tokoro et al., 1992), it is not clear whether this is the only component. This compound, (Z,Z,E)3,6,8-dodecatrien-1-ol, maintains no specificity and is followed by termite species from different families. It has been suggested that there are additional less prominent components that are specific at the species level (Kaib et al., 1982).

Other research investigating the idea that trail pheromones are multi-component blends has suggested that there two primary compounds that regulate recruitment and orientation. The recruitment component would be very short lived (Hall and Traniello, 1985) and its strength reinforced or diminished by the quality of the food resource that is associated with it (Traniello and Leuthold, 2000). The orientation component is described as more persistent, and providing long-term information for termites to navigate within the tunnel network (Hall and Traniello, 1985).

Alternatively, it is possible that trail pheromones rely more on a single active component. If a single component is responsible for foraging response, then recruitment and orientation would be dictated more by pheromone concentration. Grace et al. (1988) found that initiation of trail following, rate of movement, and distance traveled by *Reticulitermes hesperus* Banks were all directly related to the concentration of trail pheromone. Similarly, reversing direction on a trail or leaving a trail were negatively correlated with pheromone concentration. Since habituation can occur in termites from constant continuous exposure to a chemical stimulus (Grace, 1989), trail pheromone concentrations must exhibit quantitative differences within a tunnel network to prevent forager acclimation from occurring. Pheromone concentration gradients therefore appear to be necessary to maintain foraging activity and can possibly communicate directionality to areas where acceptable food sources are present.

DISCRIMINATION AMONG ESTABLISHED FORAGING SITES

It is clear that there are both naturally occurring and man-made repellents and antifeedants that interfere with termite foraging and feeding. What is less understood is why some chemical compounds that are initially non-repellent to termites are eventually avoided. How do foragers in a termite colony discriminate between food sources with apparently at least initially undetectable differences in nutritional value or toxicity?

One explanation is the tendency of termites to avoid areas where dead foragers are present. Observing foragers tunneling through agar-filled petri dishes, Su et al. (1982) discovered that when mortality from exposure to a termiticide occurred rapidly such that termites died and remained at the site of exposure, then subsequent foragers would avoid that site because of the presence of the dead foragers. This behavior was termed necrophobia (Su, 1982). This phenomenon was also described in baiting situations with the slow-acting, non-repellent toxicants abamectin and zinc borate. Laboratory assays with the latter chemicals revealed that termite mortality occurred locally around the bait sites, causing termite activity in the vicinity of these sites to cease for a period of time (Forschler, 1996). It is also possible that foragers are associating a negative outcome with the food resource. This behavior has been called associative learning (Su et al., 1995) and aversion (Thorne and Breisch, 2001) and has been implicated in the avoidance of feeding on non-repellent treatments.

The causes for recognition of and discrimination between untreated food sources and food sources treated with a non-repellent wood preservative were investigated both in the laboratory and in the field using two dimensional foraging arenas and wood treated with disodium octaborate tetrahydrate (DOT) (Campora, 2004). Results of this research indicated that foraging activity declined within areas of the tunnel network in the vicinity of the treated wood, and increased in portions of the tunnel network that contained untreated wood. Termite mortality was observed in the arenas, but dead foragers actually accumulated more in the tunnels located on the sides of the arenas that did not contain the treated wood (i.e., the areas of the tunnel network where termite activity was greatest). The positions of DOT treated and untreated wood samples were switched to assess the ability of foragers to recognize the borate treatment to which they had previously been exposed on the other side of the arenas. Foragers initiated feeding on the DOT-treated wood in the new locations, but were slow to move back into areas of the tunnel network that had previously contained treated wood.

The conclusions reached from this study were that foragers did not avoid the non-repellent borate treatment due to a necrophobic response, and they did not display learning with regard to the borate treatment specifically (i.e., learn to recognize the treated wood as undesirable). Rather, foragers responded more to the location of the non-acceptable food sources, and gradually avoided these locations. This implies that resources are mapped

within an established foraging network with respect to their acceptability. This mapping could conceivably be the result of changes in traffic within tunnels due to sublethal effects and subsequent mortality, and corresponding changes in trail pheromone concentrations within the tunnel network.

CONCLUSION

The results discussed here paint an intriguing picture of subterranean termite food location by tunneling, recruitment to newly-discovered resources, and subsequent discrimination among food resources within the tunnel network. Future advances in the study of termite foraging behavior will likely come through the application of methods in chemical ecology and in molecular genetics. Feeding and communication appear to be driven by chemistry, while molecular techniques provide new ways to study group interactions and food distribution patterns within the termite colony.

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