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Using hidden Markov models to characterize termite traveling behavior in tunnels with different curvatures

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ABSTRACT

Subterranean termites live underground and build tunnel networks to obtain food and nesting space. After obtaining food, termites return to their nests to transfer it. The efficiency of termite movement through the tunnels is directly connected to their survival. Tunnels should therefore be optimized to ensure highly efficient returns. An optimization factor that strongly affects movement efficiency is tunnel curvature. In the present study, we investigated traveling behavior in tunnels with different curvatures. We then characterized traveling behavior at the level of the individual using hidden Markov models (HMMs) constructed from the experimental data. To observe traveling behavior, we designed 5-cm long artificial tunnels that had different curvatures. The tunnels had widths (W) of 2, 3, or 4 mm, and the linear distances between the two ends of the tunnels were (D) 20, 30, 40, or 50 mm. High values of D indicate low curvature. We systematically observed the traveling behavior of *Coptotermes formosanus* shiraki and *Reticulitermes speratus* kyushuensis and measured the time (τ) required for a termite to pass through the tunnel. Using HMM models, we calculated τ for different tunnels and compared the results with the τ of real termites. We characterized the traveling behavior in terms of transition probability matrices (TPM) and emission probability matrices (EPM) of HMMs. We briefly discussed the construction of a sinusoidal-like tunnels in relation to the energy required for termites to pass through tunnels and provided suggestions for the development of more sophisticated HMMs to better understand termite foraging behavior.

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1. Introduction

Subterranean termites forage for food by building tunnel galleries below the ground that extend from the central nest to food sources (King and Spink, 1975). When constructing tunnel networks, the termites should strategically consider the limited **Q4** energy available for obtaining and transporting food resources (Lima and Costa-Leonardo, 2012; Hapukotuwa and Grace, 2012). This consideration applies to other animals as well as termites. In the field, animals can experience episodes of starvation and the prolonged starvation can sometimes lead to death. If animals survive and die as a function of variation in their foraging strategies, the natural selection has been acted in its course. The survived animals are likely to contribute genes to the next generation, while

the genes from animals that die are eliminated. In addition, many experimental or observational data have shown that the optimal foraging strategy of animals maximizes their foraging efficiency by balancing time spent feeding and time spent searching for new feeding sites and the optimization is strongly related to the stability of the animal's ecosystems (Katz, 1974; Hofbauer and Sigmund, 1998; Krivan and Cressman, 2009; Abrams, 2010). For the reasons, the foraging strategy in terms of the cost-benefit functions has been focused on ecology for more than four decades (Charnov, 1976; Pyke et al., 1977; Stephens and Krebs, 1986).

For termites, the foraging strategy is directly reflected by tunnel patterns (Robson et al., 1995; Lee et al., 2006, 2007; Tschinkel, 2010; Hapukotuwa and Grace, 2012). Thus, studying tunnel patterns is imperative for understanding of the foraging behavior and efficiency of termites, i.e., the costs and benefits of specific behaviors (Okubo et al., 1980; Shlesinger et al., 1995; Diekmann et al., 2000). **Q5**

However, there have been few studies of termite foraging behaviors or strategies as they relate to the whole termite tunnel pattern because direct observation for the foraging galleries of subterranean termites is technically difficult (Su, 2001). Thus,

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termite researchers have mainly dealt with the tunnel growth and the tunnel-tunnel interaction at the small scale (≤ 1 m) in relation to environmental factors, such as soil hardness and moisture content (Su and Lee, 2009). For examples, Campora and Grace (2001) revealed that the frequency of tunnels is uniformly distributed around the perimeter of the initiation site and the tunnel distribution is not influenced by the presence or absence of food at the foraging site. Lee et al. (2008a,b) investigated how an advancing termite tunnel responds when the tunnel meet a pre-formed tunnel with different angles. The authors revealed the relationship between the response (penetration or merging) and the angle. Haifig et al. (2011) reported that termite worker size plays an important role in determining the tunnel network architecture and both digging and the bifurcation rate. Although these small scaled experiments were valuable in understanding the termite tunneling behavior and the tunnel growth, they were still limited to comprehend the relationship between the whole topography of termite tunnel and the stability of termite ecosystem.

To overcome the observational difficulties, Lee et al. (2006) constructed a lattice model to simulate the tunnel networks of *Coptotermes formosanus* (Shiraki) and *Reticulitermes flavipes* (Kollar) based on experimental data obtained from a two-dimensional arena filled with a homogeneous sand substrate. The authors showed that the termite tunnel network has higher efficiency in food encounter rate in the clumped food distribution than in the random food distribution. The efficiency was defined as the ratio of the number of food particles encountered by tunnel to foraging time. Using a modified version of the lattice model as suggested by Lee et al. (2006), Lee and Su (2009) explored the influence of the geometry of branching tunnels on foraging efficiency (γ) for two termite species, *C. formosanus* and *R. flavipes*. They define γ as the ratio of energy gain from obtained food to energy lost by transporting food for a given time. For *C. formosanus*, a γ map consisting of two variables, the probability of tunnel branching (P_{branch}) and the probability of tunnel branch termination (P_{term}), was partitioned into three regions based on the value of γ. In the model, a probability was generated by using the uniform random function at the end of each straight segment of primary tunnel. When the value of the probability was smaller than that of P_{branch}, a new tunnel segment (branching tunnel) was introduced at the site. When another probability randomly generated at the end of the each segment of the branching tunnel was smaller than that of P_{term}, the branching tunnel growth was stopped. The γ value for *R. flavipes* was categorized as higher γ and lower γ. These results indirectly indicated a difference in foraging strategy between the two termite species. Jeon et al. (2010) developed a continuous model based on a two-dimensional tunnel network pattern. They investigated how termites could control the two variables, P_{branch} and P_{term}, in terms of tunnel network connectivity. They found that the best-simulated strategy for *C. formosanus* and *R. flavipes* termites would occur if both P_{branch} and P_{term} were simultaneously enhanced.

These simulation studies are helpful for understanding foraging behavior and strategy with regard to the whole tunnel pattern. However, they are limited in their ability to explain maximization of foraging efficiency through foraging behavior. These studies only evaluated tunnel patterns, not the traveling behaviors of individual termites. Foraging efficiency models should also include a variable representing how quickly termites travel through the tunnel network because traveling time is closely related to food transportation and return to the tunnel tip for continuous tunneling. This variable can be considered as the movement efficiency of termites (Lee et al., 2008a,b; Ku et al., 2012, 2013). In order to better understand termite foraging behavior using a simulation model, a more sophisticated model than those suggested by Lee et al. (2006) and Jeon et al. (2010) is required. An experimental study should precede the construction of such a model. There have been only a few studies that have addressed termite movement efficiency at the level of the individual. Lee et al. (2008a,b) compared the movement efficiency of advancing termites in response to right-angled corners and smooth rounded corners. They found that it takes less time for a termite to pass around a smooth rounded corner than to pass around sharp right-angled corners. This result indirectly indicates that the tunnel curvature may be an important factor in movement efficiency. Sim and Lee (2012) showed that the tunnel passing time of termites, *R. speratus* kyushuensis, decreased with decreasing tunnel width and decreasing curvature. In the present study, we additionally examined the traveling behavior of *C. formosanus* shiraki in tunnels with different curvatures. The experimental setup was same as that of Sim and Lee (2012). We systematically observed traveling behavior and measured termite speed and posture every 0.25 s. We then used the experimental data to construct a hidden Markov model (HMM) for each species in order to overcome the limitations of previous lattice-based and continuous models. HMMs are state-space models which assume that the observed distribution of the observations is conditional on a finite number of unobservable or hidden discrete states (Cappe et al., 2005). Some researchers have shown that it is straightforward to apply well-developed HMM methodology to numerous types of movement models, and outline how the basic models can be extended in different ecologically interesting and novel ways (Franke et al., 2006; Holzmann et al., 2006; Patterson et al., 2008; Pedersen et al., 2011). Franke et al. (2004) successfully simulated the movement and behavior representative of individual caribou using HMMs. Liu et al. (2011) used an HMM to elucidate the behavioral changes before and after treatment of formaldehyde (0.1 mg/L) in semi-natural conditions and showed that the HMM can be used as a powerful tool in behavioral monitoring systems.

In this study, HMMs were used to characterize individual termite traveling behavior in tunnels that had different curvatures. To evaluate the HMMs, we compared the traveling behavior generated by HMMs and that of real termites. In addition, we used the model to explore differences between the traveling behavior of the two termite species. Finally, we briefly discuss why termites construct sinusoidal-like tunnels in relation to the energy required for a termite to pass through a tunnel and suggest directions for the development of more sophisticated HMMs to enable better understanding of termite foraging behavior.

2. Materials and method

2.1. Species

Two termite species were used in this study: *C. formosanus* shiraki and *R. speratus* kyushuensis. *C. formosanus* termites (mean body lenghth: ~5 mm) were collected in Florida and *R. speratus* termites (mean body length: ~4 mm) were captured from Mt. Kyeryong, Korea. We transported the termites with the rotten wood to the laboratory and immediately separated the termites from the wood, using the methods described by Tamashiro et al. (1973). Then, we placed the termites inside a plastic chamber that contained wooden sticks as the food source. The chamber was maintained at a temperature of $28 ^{\circ}C \pm 2 ^{\circ}C$. The experiments involving each species were carried out approximately 3 months after collection.

2.2. Experimental setup

Two-dimensional foraging arenas ($9 cm \times 16 cm$) were made using Plexiglas panel, which is same with the setup of Sim and Lee (2012). In the arena, the artificial tunnels with 5 cm in length and widths (W) of 2, 3, or 4 mm were made. In the wild, termite tunnel width significantly varies according to the environmental