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MOVEMENT EFFICIENCY AND BEHAVIOR OF TERMITES (ISOPTERA) IN TUNNELS WITH VARYING PORE SIZES

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ABSTRACT

Subterranean termites (Isoptera) build tunnel networks to obtain food resources and nesting space. When tunneling, termites encounter spatial heterogeneity, such as differing soil pore space and moisture levels. This heterogeneity creates 2 types of irregularities in the tunnel surface: (1) a bumpy tunnel-wall structure caused by variable soil texture; and (2) hollow space within the tunnel, where tunnels pass through soil pores. We previously explored the response of termites to bumpy tunnel structure. In the present study, we investigated termite behavior in response to differing volumes of soil pore space. This response behavior is closely related to movement efficiency. We designed 8-cm-long artificial tunnels with hollow spaces in a 2-dimensional arena. The hollow spaces were represented as circular holes with varying diameters D (2, 3, 4, 6, 8, or 10 mm), positioned at the center of the tunnel. Tunnel widths, W, were 2 and 3 mm. We systematically observed the movement of termites (*Reticulitermes speratus kyushuensis* Morimoto) at the hole, and measured the time required (τ) for termites to pass through the tunnels. Time τ was shorter for tunnels with holes between 2 and 6 mm diameter than for those with holes of 8 or 10 mm diameter, for tunnels of both widths. Time τ was significantly different between (W, D) = (2, 10) and (3, 10). These results were explained by 3 types of behaviors. The implications of these findings are briefly discussed in relation to termite foraging efficiency.

Key Words: Termite movement efficiency; tunnel surface irregularity; termite tunnel network; foraging efficiency

RESUMEN

Las termitas subterráneas construyen redes de túneles para obtener recursos alimentarios y espacio para sus nidos. Cuando hacen los túneles, las termitas se encuentran con la heterogeneidad espacial, como diferentes espacios de poros en el suelo y el nivel de humedad. Esta heterogeneidad crea 2 tipos de irregularidades en la superficie del túnel: (1) una estructura del túnel con baches en los paredes causada por la textura del suelo variable y (2) espacios huecos dentro del túnel, donde los túneles pasan a través de los poros del suelo. Anteriormente, se estudió la respuesta de las termitas a las estructuras de túneles llenos de baches. En el presente estudio, se investigó el comportamiento de las termitas en respuesta a diferentes volúmenes de espacio de los poros del suelo. Este comportamiento de respuesta está estrechamente relacionado con la eficiencia del movimiento. Hemos diseñado túneles artificiales de 8 cm de largo con espacios huecos en una arena de 2 dimensiones. Los espacios huecos se representan como agujeros circulares con el diámetro *D* (2, 3, 4, 6, 8, o 10 mm), puestos en el centro del túnel. La anchura de túnel, *W*, fue de 2 y 3 mm. Se observó sistemáticamente el movimiento de las termitas (*Reticulitermes speratus kyushuensis* Morimoto; Rhinotermitidae) en las aperaturas, y se midió el tiempo requerido (τ) para que las termitas pasaran a través de los túneles. El tiempo, τ, fue más corto en los túneles con aperaturas entre 2 y 6 mm de diámetro que para los que tienen aperaturas de 8 o 10 mm de diámetro, para los túneles de ambos anchos. El tiempo, τ, fue significativamente diferente entre (*W, D*) = (2, 10) y (3, 10). Estos resultados son explicados por 3 clases de comportamiento. Se discuten brevemente las implicaciones de estos hallazgos en relación con la eficiencia de forrajeo de las termitas.

Palabras Clave: eficiencia del movimiento de termitas, irregularidad de la superficie del túnel; red de túneles de termitas, eficiencia de forrajeo

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Subterranean termites are social insects that form colonies often containing hundreds of thousands to millions of individuals. Colony members disperse throughout the soil, constructing underground tunnel networks up to hundreds of meters long for foraging (Su et al. 1984). Construction of the tunnel network brings a termite colony into contact with food resources sometimes with the aids of external cues such as thermal shadows (Ettershank et al. 1980). The network systems are, therefore, a record of the foraging activities of these insects. In other words, the patterns of the networks include information on the trade-offs between foraging efficiency and other biological and environmental constraints, such as the number of active foragers, soil density, and food availability (Venna & Garneshaiah 1991; Hedlung & Henderson 1999; Su and Puche 2003; Le Comber et al. 2006a, b). The trade-off is a type of foraging strategy in which termites efficiently allocate time and energy to obtaining and transporting food according to environmental conditions (Robson et al. 1995; Lee et al. 2006, 2007a). To better understand termite foraging strategy, it is important to analyze tunnel patterns in relation to the costs and benefits of constructing the tunnels (Okubo 1980; Shlesinger et al. 1995; Diekmann et al. 2000). However, few studies have addressed termite foraging behavior or strategy in relation to the entire tunnel system of a field colony because it is technically difficult to directly observe tunnel networks that may extend laterally over extensive (>1000 m^2) areas (Su, 2001).

To address this difficulty, Lee et al. (2006) proposed a simple model to simulate the tunnel networks of *Coptotermes formosanus* Shiraki and *Reticulitermes flavipes* (Kollar) using tunneling rules based on experimental data. The model was used to reveal the relationship between food encounter rate and food-size distribution pattern. Food encounter rate was defined as the ratio of the number of food particles encountered by tunnels to the number of simulation events. Results of Lee at al. (2006) showed that the food encounter rate was the highest when food resources were heterogeneously distributed. Lee et al. (2007b) created a heterogeneous landscape structure in the lattice space using a neutral landscape model (Gardner et al. 1987; With 1997) and incorporated the landscape into the lattice model for the tunnel patterns. Their simulation revealed that landscape heterogeneity strongly influences food encounter rate in the presence of high food density, and that this influence was greater for primary tunnels. These 2 studies addressed food encounter rate rather than foraging efficiency, because the encounter rate is a simpler calculation and it indirectly reflects foraging efficiency. Lee & Su (2009) explored the effect of branching tunnels on foraging efficiency, defined as the ratio of the number of food particles encountered to total tunnel length. The amount of food encountered indicates the quantity of energy obtained, and the total tunnel length represents the energy expended by termites to excavate the tunnels. Lee & Su (2009) showed that the length and frequency of branching tunnels plays an important role in foraging efficiency. Jeon et al. (2010) developed a continuous model based on a 2-dimensional tunnel network pattern. Using the model simulation, they found that the best strategy, maximizing the foraging efficiency, for *C. formosanus* and *R. flavipes* would occur if the frequency of branching and the length of branching tunnels were simultaneously enhanced.

These previous studies were helpful in understanding foraging behavior and strategy in relation to overall tunnel pattern. However, the models used in these studies did not consider the behavior of termites at the individual level, and all individuals were assumed to be identical to engage in the same tunnel-digging activity, and to have the ability to move from place to place instantaneously. Termites foraging efficiency consists of food-finding and food-transportation efficiencies (Lee et al. 2007a). Transportation efficiency relates to the speed with which termites move their food from the foraging site to their nest. Movement efficiency is closely related to food-transportation efficiency (Lee et al. 2007a; 2009), and is defined as the time taken by a termite to cover a certain tunnel distance. Obviously, termites with higher mean velocities are likely to contribute positively to transportation efficiency. For this reason, foraging efficiency used in the previous studies should be reconsidered, accounting for the role of individual termite behavior in movement efficiency.

Under field conditions, termites respond differently to local tunnel geometry (e.g., curvature and wall irregularity), which in turn strongly affects movement efficiency (Lee et al. 2008a, b). Sim & Lee (2012a, b) showed that tunnel curvature affects movement efficiency. Tunnels with a greater proportion of bends are associated with lower movement efficiency. Curvature also influences the time required to pass, when 2 termites encounter each other in the tunnel. 2 types of irregularities are common in termite tunnels: bumpy wall surfaces and hollow tunnel space. Bumpy wall surfaces may result from heterogeneity in soil properties such as particle size and moisture content (Bosma et al. 1993; Jacques et al. 1999). Tunnel walls that have lower moisture contents are likely to be more fragile, and as termite bodies or external forces contact or act on the walls, bumpy surfaces may form. In addition, large soil particles encountered by termites while tunneling are not removed, which can result in a bumpy wall surface. Hollow tunnel space can be formed via biological or physical activity (Burke et al. 1999; Zue et al. 2008). When a termite tunnel passes through soil pore spaces with diameters larger than the tunnel width, the altered geometry at the point of intersection can result in hollow tunnel space. The size and shape of this

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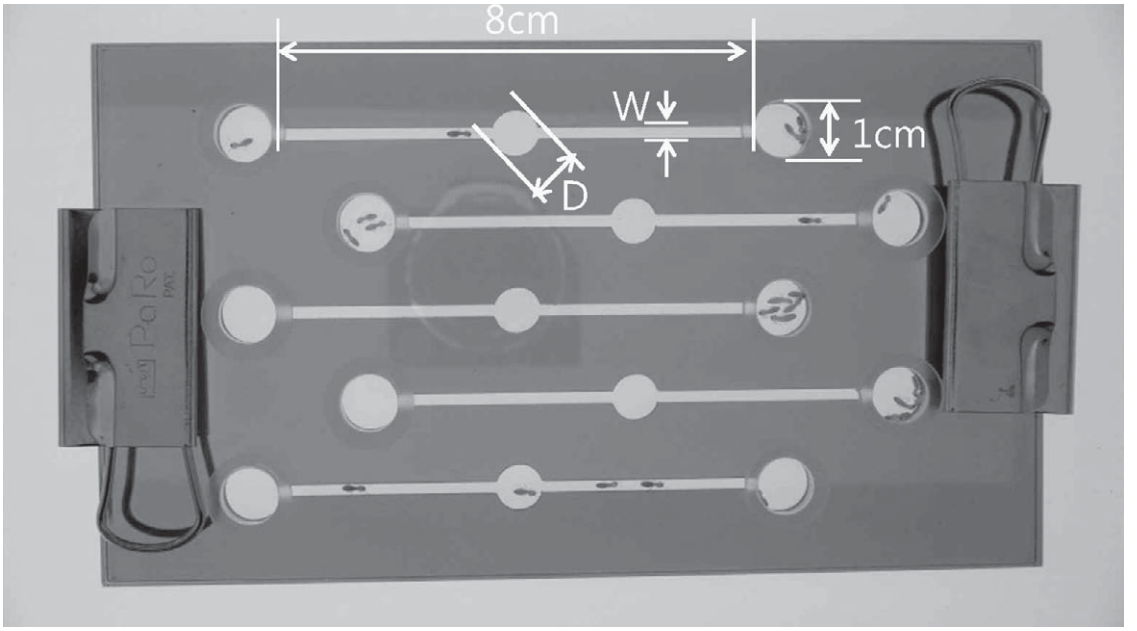


Fig. 1. Experimental arena consisting of 2 layers (16 × 8 cm, 5 mm thick) of clear plexiglas and a middle, dark gray-colored layer (16 × 8 cm, 2 mm high). The middle layer (dark gray color) includes five 8-cm-long artificial tunnels with width *W*. A circular hole with diam *D* was located at the center of each tunnel.

hollow space vary according to soil heterogeneity (Yuki et al. 2006).

To our knowledge, few studies have been conducted on the movement efficiency of termites in relation to tunnel irregularity. Ku et al. (2012), who measured time taken by termites to pass the irregularity (simplified as rectangular shapes), found 4 types of response behaviors, and termites' passing times differed according to the height and width of the irregularity.

In this study, we focused on termite movement efficiency in tunnels with different-sized hollow space. For simplification of the experiment and the interpretation of termite behavior, we considered the hollow space as a circular hole. We measured the time required for termites to pass through tunnels with circular holes of varying diameters, and carefully analyzed termite behavior in the holes.

Materials and Methods

We collected the termite *Reticulitermes speratus kyushuensis* Morimoto from dead wood at Mt. Kyeryong, South Korea. This species is widely distributed in Korea and Japan (Park & Bae 1997). Termites were immediately separated from the dead wood following the methods of Tamashiro et al. (1973), and were placed inside a chamber containing wooden sticks as a food source. The chamber was maintained at a temperature of 28 ± 2 °C.

We used a 2-dimensional foraging arena for the experiment. The experimental arena consisted of 3 layers (16 × 8 cm, 5 mm thick) of clear Plexiglas with a dark gray middle layer (16 × 8 cm, 2 mm high) between 2 outer layers. We cut linear tunnel shapes of 2 widths W (W = 2, 3 mm) in the middle layer, for the artificial tunnels. Each artificial tunnel was formed with a circular hole, representing soil pore space, at the center. The diameter of the hole, D, was 2, 3, 4, 6, 8, or 10 mm (Fig. 1). The

Table 1. Mean (± SD) time τ values (s) for termites passing through tunnels with circular holes of *W* = 2 or 3 mm, and *D* = 2, 3, 4, 6, 8, and 10 mm.

(*W*, *D*)	τ ± SD	*n*	p-value
(2, 2)	11.110 ± 2.728 a		
(2, 4)	11.993 ± 3.332 a		
(2, 6)	12.384 ± 3.876 a	100	0.000
(2, 8)	14.613 ± 4.094 b		
(2, 10)	17.683 ± 6.669 c		
(3, 3)	10.945 ± 2.871 a		
(3, 4)	12.243 ± 3.336 ab		
(3, 6)	12.728 ± 3.443 b	100	0.000
(3, 8)	14.380 ± 4.470 c		
(3, 10)	14.124 ± 4.028 c		

Note. W and D represent the tunnel width and the diam of the circular irregularity, respectively. Mean within a column followed by the same letter is not significantly different (α = 0.05; a one-way ANOVA test with Tukey's test for post hoc multiple comparison)

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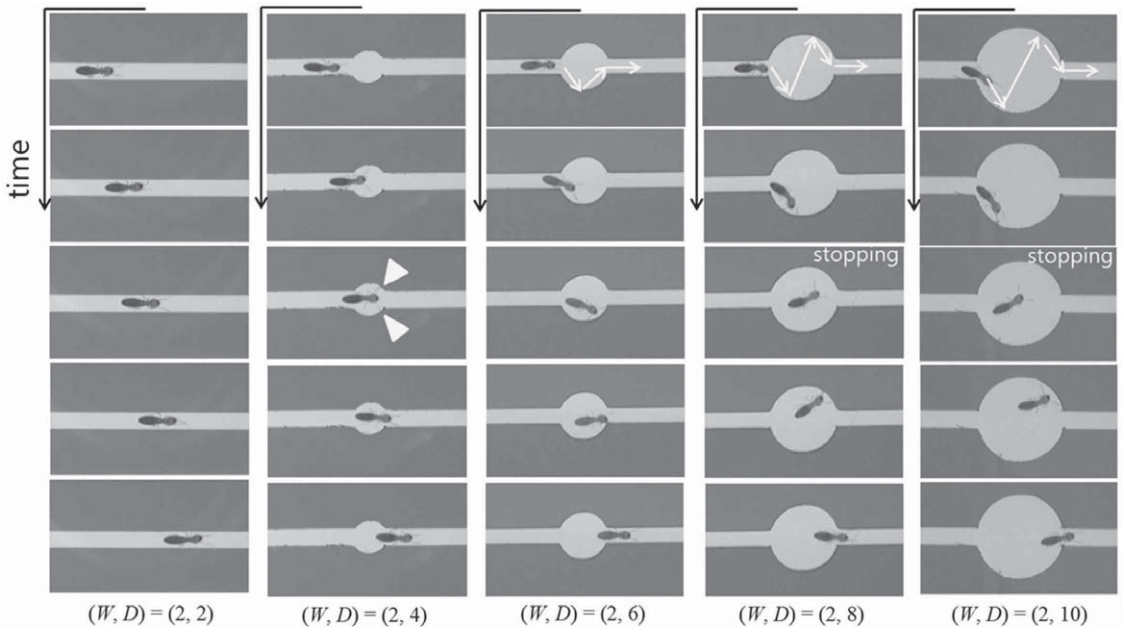


Fig. 2. Snapshots of termite walking behavior through circular holes with W = 2 mm, and D = 2, 4, 6, 8, and 10 mm. Yellow triangles indicate antennae touching the sides of the hole. Consecutive yellow arrows indicate the movement path of the walking termite. The word "stopping" indicates that a termite is showing stopping behavior at the center of the hole.

middle layer included 5 artificial tunnels. Two introduction (entry) holes (1 cm diameter) were made at the end of each tunnel.

The arenas were maintained at 29 ± 1°C, in a room with relative humidity of 40 ± 2%. Five arenas were prepared for the study. Each arena was placed in a horizontal position, and 5 worker termites were placed into each tunnel through the introduction hole. We allowed termites to acclimatize to their new environment for 12 min (Hu et al. 2003; Wilson-Rich et al. 2007) before recording their movements for one hour with a digital camcorder (SONY HDR-CX700) mounted on the top of each arena. For each combination of W and D, 25 repetitions were performed. One hundred clips showing a single termite passing through the 8-cm tunnel were extracted from each video. Data from worker termites that did not make physical contact with neighboring termites while walking in the tunnels were used in the analysis. Using the recorded video footage, we measured the time (τ) taken by each termite to pass through the tunnel. Time τ was defined as the time taken for a termite to enter and exit the tunnel.. For

TABLE 2. STATISTICAL COMPARISON OF PASSING TIME τ, FOR TUNNELS WHERE W = 2 AND D = 2, 4, 6, 8, OR 10 MM; AND W = 3 AND D = 3, 4, 6, 8, AND 10 MM.

	τ ± SD			
D	W = 2	W = 3	n	p value
2 for W = 2 3 for W = 3	11.110 ± 2.728 a	10.945 ± 2.871 a	100	0.677
4	11.993 ± 3.332 a	12.243 ± 3.336 a	100	0.596
6	12.384 ± 3.876 a	12.728 ± 3.443 a	100	0.095
8	14.613 ± 4.094 a	14.380 ± 4.470 a	100	0.701
10	17.683 ± 6.669 a	14.124 ± 4.028 b	100	0.000

Note. W and D represent the tunnel width and the diam of the circular irregularity, respectively. Mean within a row followed by the same letter is not significantly different (α = 0.05; a t- test)

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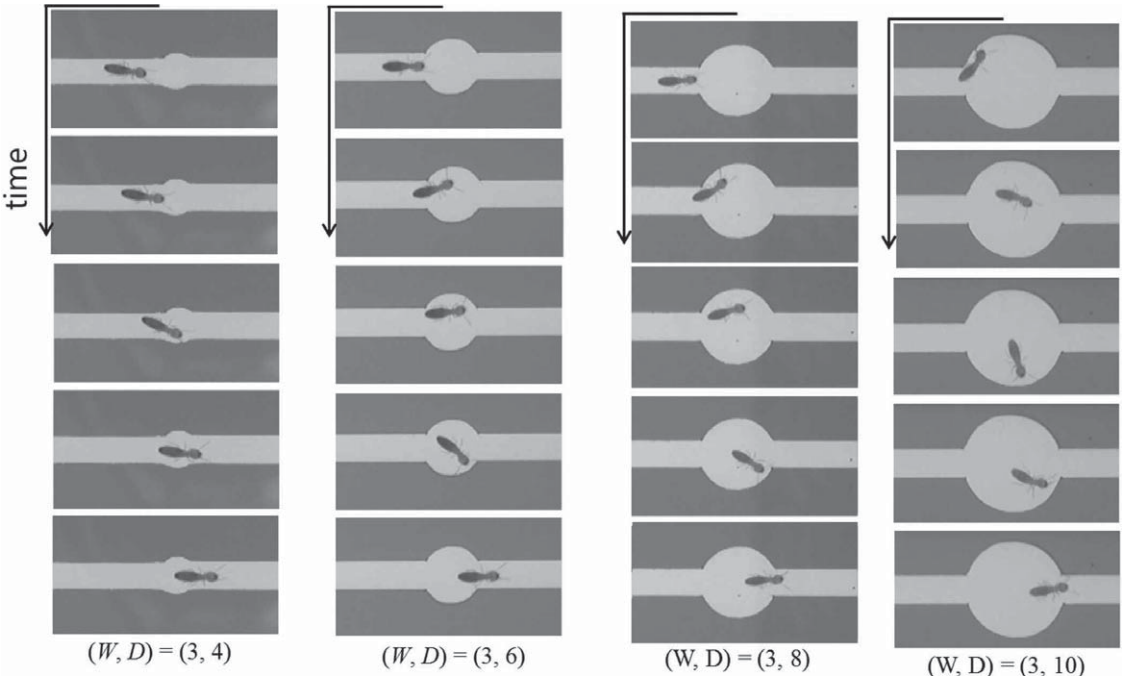


Fig. 3. Snapshots of termite walking behavior through circular holes with W = 3 mm, and D = 4, 6, 8, and 10 mm.

statistical analysis, we used a one-way analysis of variance (ANOVA) with Tukey's post hoc and Scheffe's test for multiple comparisons and applied to a t-test for statistical comparison of the tunnel passing time.

Results

Termites remained in the introduction holes for approximately 3 min, rotating along the walls. This was probably a type of exploratory behavior to obtain information of the new environment. After this initial period, termites began to move into the tunnels, touching their antennae on the tunnel walls (Lee et al. 2008b). We allowed 12 min for termites to acclimate, after which we observed their walking behavior in the tunnels. We made observations of the way in which each termite passed the circular hole positioned at the center of its tunnel.

Termites generally showed antennation behavior when walking through linear tunnels, and zigzagging behavior (Sim et al. 2012) for tunnels with W = 3 mm. For W = 2 mm, zigzagging behavior did not appear because termites did not have enough space to bend their bodies–a requirement for changing walking direction. Time duration of passage, τ. was significantly shorter for (W, D) = (2, 2), (2, 4), and (2, 6) than for (W, D) = (2, 8) and (2, 10) (Table 1). For (W, D) = (2, 2) (tunnel with no circular hole), termites walked without pausing, which resulted in a shorter passage time, τ. In the case of (W, D) = (2, 4), termites advanced into the circular hole and slightly touched the wall on the exit side of the hole (indicated by triangles in Fig. 2) without

Table 3. Mean (± SD) time values (s) required for a termite to pass through circular holes with (W, D) = (2, 8), (2, 10), (3, 8) and (3, 10). Time was measured for 2 behavioral types: those that exhibited stopping behavior at the center of the hole, and those that did not.

(W, D)	Hall passing time ± SD (with the stopping)	n	p-value	Hall passing time ± SD (without the stopping)	n	p-value
(2, 8)	4.407 ± 1.547 a	64	0.000	2.447 ± 0.631 a	36	0.000
(2, 10)	5.207 ± 2.158 b	79		2.206 ± 0.494 ab	21	
(3, 8)	3.965 ± 1.409 a	74		1.938 ± 0.572 bc	26	
(3, 10)	3.969 ± 1.423 a	75		1.540 ± 0.296 c	25	

Note. W and D represent the tunnel width and the diam of the circular irregularity, respectively. Mean within a column followed by the same letter is not significantly different (α = 0.05; a one-way ANOVA test with Scheffe's test for post hoc multiple comparison)

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TABLE 4. TERMITE BENDING ANGLES, θ (DEGREES), FORMED BETWEEN THE REAR END OF THE BODY AND THE CENTER OF THE MOUTH, FOR 2 TYPES OF WALKING BEHAVIOR: WALL-TOUCHING AND WALL-FOLLOWING.

(*W, D*)	θ ± SD (for wall touching)	θ ± SD (for wall following)	n	p-value
(2, 8)	34.13° ± 8.57° ab	19.07° ± 5.76° a	30	0
(2, 10)	37.90° ± 6.64° a	15.17° ± 4.56° b	30	
(3, 8)	29.90° ± 4.95° b	17.50° ± 4.46° ab	30	
(3, 10)	31.97° ± 4.10° b	18.10° ± 4.24° ab	30	

Note. *W* and *D* represent the tunnel width and the diam of the circular irregularity, respectively. Mean within a row followed by the same letter is not significantly different (α = 0.05; a t- test)

changing their moving direction. For (*W, D*) = (2, 6), termites bent their bodies to change their moving direction toward the left or right side of the wall. In this case, although termites changed their direction of movement toward the wall, they immediately reoriented and moved towards the exit, such that no significant increase in τ was observed (Table 1). Termites advancing to circular holes with (*W, D*) = (2, 8) also bent their bodies, and then touched one side of the wall and turned to the other side. After touching both side of the wall, termites exited the tunnels (see the movement path in Fig. 2). Interestingly, when moving from one side of the wall to the other, these termites frequently stopped at the center of the circular hole, resulting in increased τ (see Fig. 2). For (*W, D*) = (2, 10), termites showed similar behavior to that of (*W, D*) = (2, 8), but stopped for longer periods of time, further increasing τ (Fig. 2).

In wider tunnels without circular holes [(*W, D*) = (3, 3)], termites showed similar behavior to those in tunnels with dimensions (*W, D*) = (2, 2), and τ did not differ statistically between these treatments (Table 2). Time τ for (*W, D*) = (3, 3) was significantly shorter than that for (*W* = 3, *D* = 4, 6, 8, and 10). Although termites tended to walk in a zigzag motion in tunnels with (*W, D*) = (3, 3), which essentially increased the length of their path through the tunnels, they walked at higher speeds in these wider tunnels compared to those in tunnels with (*W, D*) = (2, 2), which compensated for time expended in zigzag motions. When termites encountered a hole with (*W, D*) = (3, 4), some moved through without hesitation, while others touched the walls of the hole, hesitating for a short time. This behavior caused a statistically significant increase in τ (Fig. 3). When termites advanced into holes with (*W, D*) = (3, 6), (3, 8), and (3, 10), many touched one side of the wall, turned their bodies, touched the other side of the wall, and then moved out of the hole. As for holes with (*W, D*) = (2, 10), termites spent more time, motionless, in the center of holes with (*W, D*) = (3, 10), which increased τ.

Table 2 presents statistical comparisons of τ between (*W* = 2, *D*) and (*W* = 3, *D*). No differences in τ were found among D = 4, 6, and 8. In addition, τ was statistically the same for (*W, D*) = (2, 2) and (3, 3). However, τ was significantly longer for (*W, D*) = (2, 10) than for (*W, D*) = (3, 10).

DISCUSSION AND CONCLUSIONS

Our results showed that τ was statistically shorter for (*W, D*) = (2, 2), (2, 4), and (2, 6) than for (*W, D*) = (2, 8) and (2, 10), and τ was statistically the same for (*W, D*) = (2, 2), (2, 4), and (2, 6). For tunnels with *W* = 3 mm, τ tended to increase with increasing *D*. These results can be explained by 3 types of behavior: (1) when termites encountered a small-sized hole—(*W, D*) = (2, 4), and (3, 4)—they touched the inside wall of the hole slightly, but advanced without stopping; (2) when termites encountered a medium-sized hole—(*W, D*) = (2, 6) and (3, 6)—they deviated their moving direction at the entrance of the hole to touch the left- or right-side wall of the hole, while continuing to advance without stopping; (3) for large-sized holes—(*W, D*) = (2, 8), (2, 10), (3, 8), and (3, 10)—termites touched the left- or right-side wall of the hole and then turned towards the wall on the other side. Immediately after touching both sides, termites exited the hole. In this case, when termites moved from one side of the wall to the other, they frequently stopped in the center of the hole. We speculate that in larger holes, termites would be completely separated from the wall when they moved from one side to the opposite side, and in the absence of a wall to guide their walking they may have lost the tactile cues and stopped walking. For holes with *D* < 8 mm, termites were almost in contact with the wall as they passed through the hole. We performed a statistical comparison of hole-

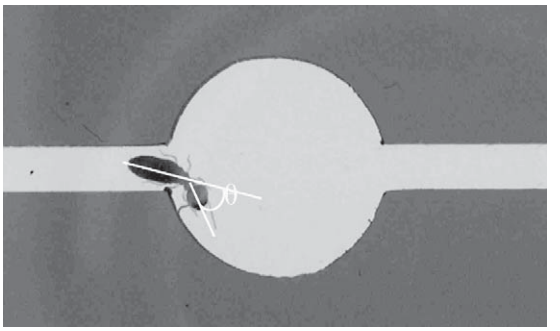


Fig. 4. Snapshot representing the bending angle, θ, of a termite at the entrance of a circular hole.

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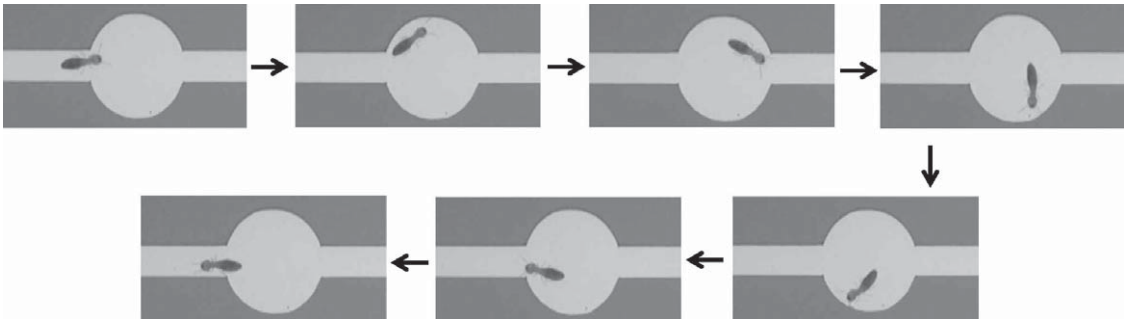


Fig. 5. Wall-following and turning behavior of termites in circular holes with (W, D) = (3, 10).

passing time for 2 cases, D = 8 and 10 mm: one in which a termite passed through the hole without stopping at the center; and one in which a termite stopped in the hole before passing through (Table 3). The results showed that stopping behavior strongly contributed to an increase in τ, suggesting that if tunnels intersect many larger-sized soil pores, termites› movement efficiency is likely to decrease. Because movement efficiency was defined as the time required for a termite to move between 2 defined points (Lee et al. 2008), an increase in τ would have a negative influence on foraging efficiency. In order to avoid this stopping behavior, termites may use a strategy in which they reduce hole size to a width that is compatible with their body size. Lee et al. (2008a) reported that when termites excavate tunnels, they move the excavated soil into a sharp-angled corner to avoid decreasing their movement efficiency. This soil-filling behavior could also occur when termites encounter large soil pores. It would be interesting to experimentally investigate filling behavior in relation to soil pore size.

As shown in Table 3, intriguingly, termites paused longer in tunnels where (W, D) = (2, 10) than in tunnels where (W, D) = (3, 10). Considering that the hole size was the same in both cases, the cause of this time difference is perplexing. We conjecture that for termites advancing from narrower tunnels, the 3 mm hole size may be relatively larger, which in turn may cause them to pause longer at center of the hole so as to acclimate to the perceived larger hole.

As shown in Figs. 2 and 3, most termites placed in tunnels where (W, D) = (2, 8), (2, 10), (3, 8), and (3, 10) touched one side of the wall, turned, and moved towards the other side of the wall. On the other hand, some termites in the same-sized tunnels showed wall-following behavior without turning towards either side. We measured the termites' bending angle, θ, for termites exhibiting wall-touching behavior in the hole, and those demonstrating wall-following behavior (Table 4). The bending angle was measured between the rear end and the center of the mouth (Fig. 4). The results indirectly indicate that bending angles of 30-40° may break the wall-following behavior. When θ is less than $\approx$ 20°, termites showed wall-following behavior along a semi-circular path and then exited the holes. This critical angle may be related to the degree of curvature of termite tunnels. Curvatures sharper than the critical angle are likely to cause a decrease in movement by obstructing wall-following behavior.

In addition to these behaviors, we observed that when termites met a relatively large-sized hole, as in (W, D) = (2, 8), (2, 10), (3, 8), and (3, 10), they frequently reversed their movement direction (Fig. 5). In most cases, this behavior occurred when termites showed wall-following behavior along the semi-circular path (Fig. 5).

Although our study was conducted using a small-sized arena and a simple-shaped irregularity to represent soil pore space generated by biological or physical factors, the data provide valuable insights into behavioral mechanisms of increasing movement efficiency. Our results are particularly useful for designing future experiments that require construction of an individual-based model (IBM) for studying termite behavior in tunnels (Lee & Su 2010). The individual approach requires application of object-oriented (or agent-based) modeling, which is closely related to the modeling that utilizes the behavioral repertoire of interactions between individuals, and between individuals and environmental conditions. The behavioral repertoire determines individual actions. IBMs may include life cycles of individual termites, competitive interactions among species, and complex environmental system dynamics. An important behavioral rule for an IBM is likely to be the termites' behavioral response to an irregularity, such as a soil pore, in relation to movement efficiency. This study provides new directions for empirical investigations of termite foraging efficiency as it relates to the termites' behavioral responses to soil pore space.

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