Trunk Trail Foraging of the Fungus-Growing Termite *Macrotermes carbonarius* (Hagen) in Southeastern Thailand

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ABSTRACT  The temporal and spatial change of foraging activity of *Macrotermes carbonarius* (Hagen) was studied in a durian orchard of southeastern Thailand. This termite is the only open-air foraging species of the fungus-growing Macrotermitinae. Workers constructs "pavement" trackways on the ground, which are used as trunk trails to connect foraging holes to foraging sites. This is the first paper to show the trunk trail foraging in fungus-growing termites. The major workers made pavement trackways paved with soil and fecal pellets which open-air foraging columns used for traveling to the foraging area. The pavement trackway was longer than the subterranean gallery. Foraging workers spread from the end of the pavement trackway onto the foraging area, where they picked up dead grass from the ground surface and carried it into the foraging hole. The soldiers led the advancing column to a foraging site and guarded both sides of the column, facing away from the column's edge. The outskirts of foraging area were guarded by minor and major soldiers and several minor soldiers always went ahead of the column, playing the role of scouts. Foraging took place only in the dry season and at night, and foraging areas were changed irregularly. In most instances, a single foraging site and one foraging hole was used for each foraging bout. The same pavement trackways and foraging sites were rarely used for two consecutive days.

Key Words: *Macrotermes carbonarius* / Isoptera / fungus-growing termite / open-air foraging / trunk trail foraging

Termites are one of the most important soil macrofauna in tropical terrestrial ecosystems. Their maximum density and biomass reaches 4000-5000/m² and 10gww/m² respectively (Wood & Sands, 1978). They consume 22-29% of annual leaf litter supply in the tropical rain forest of Malaysia (Matsumoto & Abe, 1979) and 63% of annual grass litter supply in the savanna of Nigeria (Collins, 1981).

The foraging behavior of termites is not easy to observe, because most species nest and forage in wood or soil and construct subterranean or surface galleries from their nests to foraging sites. However, some groups of termites adopt an "open-air" foraging behavior. In the Termitidae, three groups of termites show regular open-air foraging in Southeast Asian forests: two groups of Nasutitermitinae (*Longipeditermes longipes* [Haviland], and the closely related genera *Hospitalitermes* and *Lacessititermes*), and a species of Macrotermitinae *Macrotermes carbonarius* (Hagen); (Jander & Daumer, 1974). No information is available on the foraging pattern of *M. carbonarius*, although the foraging behavior of *Hospitalitermes* and *Longipeditermes longipes* has been reported by Jander & Daumer (1974) and Collins(1979).

*M. carbonarius* is a large black, fungus-growing termite occurring in Southeast Asia (Snyder, 1949). The species constructs a conspicuous large mound, consuming fallen leaves

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and small branches (Abe, 1979). The results of earlier studies suggest that the tropical rain forests of West Malaysia support a high biomass of *M. carbonarius* (Matsumoto, 1976; Abe & Matumoto, 1979; Matsumoto & Abe, 1979). Population size of a colony with a large mound was estimated at approximately 88,000 (Matsumoto, 1976).

This paper examines temporal and spatial changes in the above-ground activity of *M. carbonarius* in a durian orchard of southeastern Thailand.

### MATERIALS AND METHODS

*M. carbonarius* is widely distributed in the Malay Peninsula, Thailand, Cambodia, and Burma (Snyder, 1949). It forms a huge subconical mound reaching up to about 2-3 m in height in Thailand (Watanabe et al., 1984). The nest proper is located in the lower-central area of the mound, and many fungus combs are situated in chambers in the peripheral part of the mound. Small fragments of fallen leaves and wood are stored on the floor of wide galleries situated in the lowest part of the nest (Abe, 1978).

The present study was conducted in the grassy area of durian orchard in the Trat Province (12°30'N and 102°15'E) of Thailand. An area of 20m × 20m including a small mound (40cm in height, 3m² in basal area) of *M. carbonarius* was selected for the observation of foraging behavior. The ground surface in this area was covered with grasses, mostly *Paspalum conjugatum, Imperata cylindrica* and *Brachiaria reptans*.

The observation carried out every night (18:00-06:00) from August 26 to September 15 (rainy season) and from November 29 to December 22 (dry season), 1984. Routine censuses involved scanning the study area with a flashlight. Pavement trackways and foraging areas were checked and recorded on a map every night.

### RESULTS

The system of foraging passages

Fig. 1 schematically shows the system of foraging passages (subterranean gallery, pavement trackway and foraging area) of *M. carbonarius*. Each subterranean gallery, which extended radially 1 to 3 m from the nest, was located at about 20 cm below the soil surface (3-5 cm width) around the nest proper and rose steeply near the pit about 3 to 5 cm below the soil surface (2-3 cm width). After foraging, many dead grass fragments were observed in the pit (15 cm × 5 cm × 3 cm).

The pit led to the foraging hole which major workers sealed with soil in the day and

![Fig. 1. Schematic representation of the foraging passages of *M. carbonarius*.](image)
opened at night. Pavement trackway extended from the foraging hole to the foraging area. *M. carbonarius* formed foraging columns and traveled upon the pavement trackway to the foraging area where foragers spread out.

**Process of trunk trail foraging**

Foraging periods of *M. carbonarius* were 20:45-4:53 on December 14-15, 19:50-6:25 on December 15-16, 19:45-6:25 on December 17-18, 19:50-5:10 on December 20-21, 19:40-6:15 on December 21-22. The temporal change of foraging activity on December 15-16 is shown in Fig. 2. Termites foraged in the night from an hour after sunset to dawn for about 10 hours. A similar temporal change of foraging activity was observed on the other days.

Foraging columns were composed of major workers, major soldiers and minor soldiers, but minor workers were not involved. Based on 7 night-time observations from November 29 to December 22, the process of foraging was divided into 5 stages (Fig. 3).

**Stage 1: Beginning of foraging**

The termites traveled from the mound by way of subterranean galleries to the soil surface where they emerged through foraging holes. Within an hour after sunset, one to three circular foraging holes (3 cm in diameter) were opened within a radius of 1 to 3 m from the mound. Two to three major workers opened the holes by breaking a plug of soil. Two to three minor soldiers emerged first, taking up outward-facing positions at the hole edge while maintaining vigorous antennal movement. This was followed by the emergence of 10 to 20 minor and major soldiers (14 minor soldiers and 6 major soldiers on December 14), forming the head of foraging column. These soldiers led the advancing column to a foraging site and some following soldiers separated successively to the both sides of the column. They guarded both sides of the column, facing away from the column's edge. Several minor soldiers always went ahead of the column, playing the role of scouts. The column was joined by major workers
Stage 1

Stage 2

Stage 3

Stage 4

Stage 5

Fig. 3. Five stages in the process of trunk trail foraging. The triangles signify termites and direction of movement. 1) Beginning of foraging, 2) Constructing pavement trackway, 3) Collecting food, 4) Withdrawing from foraging area, 5) Termination of foraging.

when the first group of soldiers had extended the column for about 10 cm from the hole. Moving speed of the head of the column was about 1.5 cm/min. during the orientation on December 14 (20:30-21:00).

Stage 2: Constructing pavement trackway
As the number of foraging termites in the column increased, 30-40 major workers (about 80% of the major workers of column, observation on December 17) separated from the column of termites and began to pave the central part of the foraging path (3 to 5 cm width) with soil
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and fecal pellets. This pavement trackway (2 to 5 cm width, 2 to 4 mm thick) could usually be detected for at least one week, although they were collapsed easily on rainy days. Usually a pavement trackway was constructed from each foraging hole. It was easily distinguished from the adjacent soil surface by its smooth surface (Fig. 4-A).

The soldiers and foraging workers traveled to the foraging area along the pavement trackway. Many workers that had engaged in paving returned to the foraging hole quickly after plastering pellets of soil without going to foraging area. The lateral lines of the column as well as the foraging hole were guarded by stationary minor and major soldiers which were distributed rather uniformly at intervals of 1 to 2 cm (Fig. 4-B).

At this stage, the walking speed of workers was about 8 cm/min. (December 14, 21:30-22:00). The pavement trackway divided into several short branches before terminating.

Stage 3: collecting food

The termites of an orderly column became scattered after leaving the end of the pavement trackway. Termites dispersed widely and the front line spread radially to forage. The outskirts of the foraging area were guarded by minor and major soldiers. They were distributed at an interval of 2 to 4 cm. The foraging area expanded with time as foraging workers spread out rather uniformly in the foraging area (Fig. 4-C). Foraging area, length of pavement trackways and number of foraging holes are shown in Table 1. Maximum length of the pavement

Fig. 4. Foraging behavior of M. carbonarius. A) Pavement trackway, B) Foraging column guarded by minor and major soldiers, C) Workers and soldiers of outskirts of foraging area, D) Foraging workers climbing up dead grass.
Table 1. Foraging area, length of pavement trackways and number of foraging holes in December, 1984.

<table>
<thead>
<tr>
<th>Date</th>
<th>Foraging area (m²)</th>
<th>Total length of trackways (m)</th>
<th>Number of trackways</th>
<th>Number of foraging holes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dec. 1</td>
<td>1.09</td>
<td>0.95</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>4</td>
<td>0.62</td>
<td>1.65</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>14</td>
<td>0.58</td>
<td>1.70</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>15</td>
<td>6.68</td>
<td>5.20</td>
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<td>17</td>
<td>7.34</td>
<td>6.05</td>
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<td>1</td>
</tr>
<tr>
<td>20</td>
<td>4.82</td>
<td>6.05</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>21</td>
<td>13.35</td>
<td>6.95</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

Trackway was 6.95 m, and maximum foraging area was 13.35 m².

Foraging workers picked up dead grass on the ground surface in the foraging area. They cut the grass into small pieces (3 to 15 mm in length) before carrying it into the foraging hole. Termites were occasionally observed to climb standing dead grass and cut it down before carrying it to the foraging hole (Fig. 4-D).

Soldiers defended foraging workers against attack by the Ponerine ant *Pachycondyla* sp. which foraged singly and captured lone workers. Five workers were attacked and carried off during the overnight observation on December 14.

The column appeared to be controlled by an efficient traffic rule: homing workers marched in two center lines, while outgoing workers used two lateral lines on the pavement trackway. Walking speed of foraging workers on the trackway was 1.8 cm/sec (homing workers, n=20) and 1.5 cm/sec (outgoing workers, n=20) on December 18 (0:00-0:30).

**Stage 4: Withdrawing from the foraging area**

About 30 minutes before dawn, the number of outgoing workers decreased abruptly and the foraging area gradually decreased. Workers stopped foraging and went back to the foraging hole along the pavement trackway. They were followed by the minor and major soldiers that were guarding the outskirts of the foraging area. These soldiers walked backward to the pavement trackway, keeping their head toward the outside of foraging area, playing a role of rear guards of withdrawing workers. Thus the foraging area was gradually reduced. These soldiers turned their heads and returned to the foraging hole when they arrived at the pavement trackway. The soldiers forming lateral picket lines stayed in position until all members of the withdrawing column had passed, at which time they turned head and followed the end of the withdrawing column in order of the end of picket lines.

**Stage 5: Termination of foraging**

After all members of a foraging column withdrew into the foraging hole, two or three minor soldiers appeared to search for stragglers. The foraging hole was guarded by minor and major soldiers until the last straggling worker returned to the hole. The hole was closed by major workers after all the guarding soldiers withdrew.

Immediately after closing the foraging hole, enormous numbers of the myrmicine ant *Pheidologeton* sp. (hundreds or thousands of individuals) wandered around the hole on December 5. The ants arrived at the foraging hole by using the pavement trackway. On December 17, the ants reached the hole before closing of the hole and attacked termite
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workers which were closing the hole. However, soldiers positioned around the hole threatened the ants by shaking their mandibles up and down, thus managing to keep ants from the hole. The foraging hole was then closed by major workers without being attacked.

Temporal change of foraging activities and foraging sites
Foraging activities of *M. carbonarius* in the rainy and dry seasons are shown in Table 2. The termite was not observed to perform an open-air foraging in the rainy season (August 26 -
Table 2. Foraging activity of M. carbonarius in the rainy and dry season.

<table>
<thead>
<tr>
<th>Rainy season</th>
<th>August</th>
<th>September</th>
</tr>
</thead>
<tbody>
<tr>
<td>Foraging activity</td>
<td>- - - - - - - - - - - - - - - -</td>
<td>- - - - - - - - - - - - - - - -</td>
</tr>
<tr>
<td>Rain fall</td>
<td>C C R R R R R R R R R C C C R R R R C</td>
<td>C C C C C C C C C C C C C C C C</td>
</tr>
<tr>
<td>A/o dead grass</td>
<td>- - - - - - - - - - - - - - - -</td>
<td>- - - - - - - - - - - - - - - -</td>
</tr>
<tr>
<td>Note</td>
<td>M</td>
<td>M</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Dry season</th>
<th>November</th>
<th>December</th>
</tr>
</thead>
<tbody>
<tr>
<td>Foraging activity</td>
<td>- - - - - - - - - - - - - - - -</td>
<td>- - - - - - - - - - - - - - - -</td>
</tr>
<tr>
<td>Rain fall</td>
<td>C C C C C C F F F F F F F F R R F F F F</td>
<td>C C C C C C C C C C C C C C C C</td>
</tr>
<tr>
<td>A/o dead grass</td>
<td>+ + + + + + + + + + + + + + + + + + + +</td>
<td>+ + + + + + + + + + + + + + + + + + + +</td>
</tr>
<tr>
<td>Note</td>
<td>M M M</td>
<td></td>
</tr>
</tbody>
</table>

Foraging activity: + --- open air foraging ± --- appear on the ground but no foraging - --- no open air activity.

Rain fall: F --- fine weather C --- cloudiness R --- rain R' --- shower.

A/o dead grass: + --- rich - --- poor.

Note: M --- construction of the mound.

September 15), while seven separate foraging events were observed in the dry season (November 29 - December 22).

Daily changes of foraging sites and pavement trackways are shown in Fig. 5. The termites used a single foraging site for each foraging bout and, with the exception of December 21, did not use the same pavement trackways and foraging sites on two consecutive days.

The termites made only one foraging hole for each foraging except for December 15 when three holes were used. The same foraging hole was often used on several occasions, e.g. December 1 and 17, December 4 and 14, December 20 and 21. However, foraging sites did not overlap except for the foraging on December 20 and 21.

DISCUSSION

Few papers show the spatial foraging pattern of termites at the colony level, although many studies have been conducted on the feeding activities of termites (reviewed in Wood & Sands, 1978; Josens, 1985). Foraging of M. carbonarius took place nocturnally during the dry season. Similar patterns have been reported in other species of Macrotermes in Africa (Lepage, 1983). The most important finding is that M. carbonarius constructed pavement trackways as trunk trails for foraging on the ground, and changed daily foraging areas irregularly. Trunk trail foraging has been reported in some ants. They make trunk trails above ground from their nests to the foraging areas; e.g. harvester ant Pogonomyrmex barbatus (Gordon, 1991), and a leaf-cutting ant Atta colombica (Shepherd, 1982). They speed travel over normal rough terrain by smoothing the surface and removing obstacles and they are more easily defended against predators (Brian, 1983).

Foraging systems in Macrotermes

In the present study, I observed that M. carbonarius used open air foraging (on the pavement trackways) from foraging hole to foraging area with the column length being greater than that
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Fig. 6. Three types of foraging system in Macrotermes. The relative length of subterranean galleries and the above ground foraging passages are shown schematically.

Type 1: subterranean gallery only (e.g. M. malaccensis)
Type 2: subterranean gallery > above ground (e.g. M. michaelseni)
Type 3: subterranean gallery < above ground (e.g. M. carbonarius)

of the subterranean gallery leading from nest to foraging hole. This is an atypical foraging system for Macrotermes. M. michaelseni in the grassland of Kenya extends subterranean galleries up to 50m from the nest (Darlington, 1982), and above ground foraging passages are much shorter than subterranean galleries (Abe, personal communication). M. malaccensis in the tropical forest of Malaysia does not form above ground foraging passages (Abe, 1978).

Thus at least three types of foraging systems of Macrotermes can be distinguished in relation to the relative length of subterranean galleries to above ground foraging passages as shown schematically in Fig. 6: 1) malaccensis type (subterranean), 2) michaelseni type (subterranean > above ground), 3) carbonarius type (subterranean < above ground). Body coloration is different between the foraging systems; malaccensis (light reddish brown), michaelseni (dark reddish brown), carbonarius (black). All species of Macrotermes, except for M. carbonarius, seem to have evolved the foraging system Type 1 or 2.

Adaptive significance of trunk trail foraging strategy of M. carbonarius

The efficiency of a given foraging strategy in termites is determined by the ratio of energy required during foraging (Ef) to energy acquired as a result of collecting forage (Ec) i.e. Ec:Ef. While Ec is relatively easy to calculate, Ef is more difficult comprising,

1) Ep; energy loss due to predation,
2) Eg; energy consumed during pavement and/or subterranean gallery construction,
3) Et; energy consumed during food collection by workers and soldiers,

i.e., \( Ef = \Sigma (Ep + Eg + Et) \).
Therefore, while the efficiency of termite foraging strategies may be relatively constant between species, the relative size of the components of Ef will vary between species, depending on the foraging strategy involved.

*M. carbonarius* mainly consume leaf litters, while *M. malaccensis* mainly consume fallen large branches in the tropical rain forest of Malaysia (Abe, 1979). *M. michaelseni* is intermediate, collecting various kinds of materials: dead grasses, living grasses, fallen twigs, fallen branches and dung of herbivorous mammals (Abe & Darlington, 1985). Thus, the termites using relatively long subterranean galleries tend to utilize relatively large mass of food such as wood. Large mass of food seemed to be good for long period foraging at the same place. The termites may counterbalance the high cost of *Eg* with long period foraging. In the present study area, *M. carbonarius* collected dead grasses only in the foraging. Although dead grasses are scattered as compared with fallen twigs and fallen branches, they tended to be distributed uniformly and supplied regularly. Therefore, the strategy to shift the foraging sites frequently may be better than to forage at the same place for a long time in order to collect dead grasses efficiently. The *carbonarius* type foraging system is easier to change the foraging site, because cost of *Eg* is lower than other *Macrotermes*. The distributional pattern of available resource seems to be important for the evolution of foraging strategy.

On the other hand, open-air foraging system with pavement trackway may not only suffer high predation on the ground surface but also permit predatory ants to invade the nest proper easily through the subterranean galleries because pavement trackway makes it easy for predators to reach foraging hole and the relative distance between hole to nest proper is short. In fact, an enormous number of the myrmicine ant, *Pheidologeton* sp., wandered around the foraging hole along the trunk trail of *M. carbonarius*. If predatory ants invade into the nest proper, the colony may suffer high mortality. In the mature colony of *M. michaelseni*, the invasion of subterranean doryline ants is the main cause of colony mortality (Darlington, 1985), because they invade the nest and kill reproductives using long subterranean galleries as access routes (Abe & Darlington, 1985).

I suggest that the foraging pattern of *M. carbonarius*, which makes one foraging hole for each trunk trail and changes daily foraging areas irregularly, may be effective to avoid predation.

ACKNOWLEDGMENT I wish to express my sincere thanks to Drs Siriwat Wongsiri, Usanee Yodyingyud (Chulalongkorn University) and Prof. Moritaka Nishihira (Tohoku University) for their encouragement and advice during this study. I extend my thanks to Prof. Takuya Abe (Kyoto University) and Dr. John A. Holt (CSIRO) for kindly reading manuscript and discussion.

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Received July 25, 1994
Accepted Jan. 18, 1995
杉尾幸司 タイ国南東部に生息するキノコを栽培するシロアリMacrotermes carbonarius (Hagen) の幹蟻道を使った採餌活動

*Macrotermes carbonarius* は、キノコを栽培するシロアリのなかで唯一地上歩行をして採餌を行う種である。本種の採餌活動を明らかにするため、採餌活動の時間的・空間的変化についてタイ国南東部で調査した。その結果、採餌に際して以下のような活動を行うことが確認できた。

採餌のために地面に空けた穴から *Major worker* が次々と地面に現れ、土と肛門より出した物質で地面を舗装して道をつくった。この舗装された道は、地面の穴から採餌場をむすぶ幹蟻道として利用され、採餌のために地上歩行をする行列はこの道の上を通って採餌場に向かった。行列の中心には採餌活動を行う2〜4列の *Major worker* が位置し、先頭と両側は *Soldier* によって守られていた。*Major worker* は舗装された道の終点に達すると採餌場の各所に分散して餌を捜し、地面に落ちている枯草などを呑んで再び舗装道上の行列に合流して餌を巣に運びこんだ。また、採餌場の外周も *Soldier* によってガードされており、採餌の範囲を広げる際にも常に *Soldier* が先頭であった。

採餌を行うのは夜間だけで、これらの活動は乾期にのみ確認できた。一晩のうちに同時に数ヶ所の採餌場所で活動を行うことはなく、各々の採餌は1ヶ所の採餌場を利用して行われた。また、採餌場所は頻繁に変えるため同じ幹蟻道や採餌場所を2日以上連続して使用することはまれであった。