

Behavioral and Morphological Changes in Soldiers of *Macrotermes gilvus* (Termitidae: Macrotermitinae) Parasitized by *Misotermes mindeni* (Diptera: Phoridae)

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ABSTRACT *Misotermes mindeni* Disney and Neoh is a solitary endoparasitoid of *Macrotermes gilvus* (Hagen) (Termitidae: Macrotermitinae), exclusively parasitizing the head of major soldiers. In this study, behavioral and morphological changes in the parasitized termite host were evaluated. We also observed the larval parasitoid emerging from the host. We found that parasitism mainly occurred in termite mounds overgrown with grass and mounds that had been broken up previously for other experiments. The parasitized soldiers showed a significantly lower level of interspecific aggressiveness compared with healthy soldiers ($P < 0.05$). Parasitized soldiers also changed in habitat preference to one isolated chamber of the nest. This might be an adaptive strategy that facilitates parasitoid dispersal, provides protection to parasitoids, and reduces the risk of parasitism to host colony. An abnormally rounded head capsule and remarkably short mandibles are characteristics of a parasitized soldier. The older larval fly stages were found only in major soldiers. We suggest that parasitization may first start in fourth or even earlier larval termite instars. The fly larva develops in the termite soldier's head capsule and pupates inside the host's body.

KEY WORDS Diptera, parasitism, termites, *Macrotermes gilvus*, *Misotermes mindeni*

Phorid flies have a wide range of larval feeding habits. Generally, they are scavengers, saprophages, and feeders on organic decaying matter (Askew 1971, Brown 1992). The life histories of phorid flies vary (Ferrari 1987). Larvae may be parasitoids of living plants and fungi, predators of insect eggs and larvae, or parasitoids or symbionts of social insects (Brown 1992). Of the $\approx 3,000$ described species covering 250 genera (Brown 1992), 300 species are endoparasitoids of arthropods in soil, for example, termites, ants, and millipedes (Eggleton and Belshaw 1992, Disney 1994). Some parasitoids are solitary, producing only one adult per host, whereas others are gregarious, producing several adults per host (Strand 1989).

Competition for resources between the host and the immature parasitoid contributes to behavioral and physiological changes in the host. Changes in hosts include alterations of morphology (Trabalon et al. 2000), feeding behavior (Thompson and Redak 2008), aggressive behavior, movement, development, activity patterns, and habitat preferences (Brodeur and Boivin 2004, Sze et al. 2008). We studied these changes in a termite parasitized by phorid larvae.

Macrotermes gilvus (Hagen) (Termitidae: Macrotermitinae) is a mound-building termite species that is widespread in Southeast Asia (Roonwal 1970). It is an

agricultural pest of sugarcane fields (Roonwal 1970, Cowie et al. 1989) and also a secondary pest of buildings after the suppression or elimination of predominant *Coptotermes* spp. (Lee 2007, Lee et al. 2007). Size dimorphism is exhibited in both worker and soldier castes. In *Macrotermes*, soldiers can exhibit deformation of the head capsule and mandibles. These soldiers are parasitized by dipteran parasitoids (Sze et al. 2008, Neoh and Lee 2009b).

Species in the dipteran families Phoridae and Caliphoridae parasitize *Macrotermes* (Kemner 1925, Disney and Kistner 1990, Sze et al. 2008, Neoh and Lee 2009b). There are detailed studies of termite-fly associations (Disney 1986; Disney and Kistner 1990, 1992; Disney and Darlington 2000), but effects of parasitism on the termite host have received little attention. The objectives of this study were to evaluate the behavioral and morphological changes in *M. gilvus* hosts induced by parasitism by the fly *Misotermes mindeni* Disney and Neoh and to describe how the larval parasitoid emerges from the host.

Materials and Methods

Parasitism Surveillance. We surveyed all *M. gilvus* mounds at the following two locations. (1) Minden Campus of the Universiti Sains Malaysia (USM) (5°21'N and 100°18'E). *M. gilvus* was the most com-

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mon mound-building termite species found on the campus, account for 43.7% of the total termite mound ($n = 978$). (2) Three kilometers on each side of the road of Bayan Lepas (5°17' N and 100°15' E). Both locations were ≈8 km apart in Penang on the north-eastern coast of Peninsular Malaysia. Parasitism rates of 23 (number of mounds examined, $n = 44$) and 73% ($n = 15$) were recorded from the USM and Bayan Lepas sites, respectively.

We categorized the examined mounds as follows: disturbed (mounds that was earlier broken up intentionally for experimental purposes); less active (mounds that were covered by vegetation and were partially eroded); or active (mounds that showed new mound extensions). Termite mounds were broken up by digging a trench around the base of the nest and applying sideways force to remove the outer layer casing. Under the casing, the hive was revealed to contain fungus combs, where the termites tended to aggregate. Parasitized soldiers that possessed a conspicuous rounded head capsule and a pair of short mandibles and nonparasitized soldiers were collected ($n = 50$, respectively).

Aggressive Behavior. A parasitized soldier of *M. gilvus* and a healthy soldier of *Macrotermes carbonarius* (Hagen) (Blattodea: Termitidae) were paired in a 50-mm-diameter petri dish with 50-mm-diameter moist filter paper on the bottom under laboratory conditions (26.4 ± 0.1°C and 63 ± 1% RH). The termites were acclimatized for 5 min before the test. The two sibling species often compete and fight in nature. This experiment was run with 10 different pairs of termites. As a control, confrontation between healthy soldiers of both species was conducted ($n = 10$). The pairs were video recorded for 5 min. Behaviors were analyzed using the following definitions described by Jmhasly and Leuthold (1999): (1) examination or antennation (contact between antennae or between antennae and body); (2) alarming (jerking, a repeated rapid body movement that moves the body front and back) and/or avoidance (chasing or escaping); and (3) aggression (mandibles open, seizing, or biting). The behaviors of the soldiers were recorded in 10-s intervals (thus 30 observations for each pair). The frequencies of each behavior were pooled and averaged per 10 s. We compared the aggressiveness of healthy soldiers and parasitized soldiers using pairwise Mann-Whitney *U* tests followed by a Kruskal-Wallis test to compare the behaviors displayed by parasitized soldiers.

Determination of Parasitized Host Stages. Healthy minor ($n = 10$) and major soldiers ($n = 10$) and parasitized major soldiers ($n = 20$) were randomly chosen for biometric analysis. Specimens preserved in 70% alcohol were measured under an Olympus SZ61 stereo microscope (Olympus, Tokyo, Japan) with IC Imaging Standard V2.1 (The Imaging Source Europe, Bremen, Germany) and measured using Analysis Image Processing Software (Soft Imaging System, Münster, Germany). We took the following measurements based on earlier descriptions by Neoh and Lee (2009a): (1) maximum head width; (2) width of head

Table 1. Aggression behaviors of parasitized soldiers and healthy soldiers of *M. gilvus*

Behaviors	Parasitized soldiers	Healthy soldiers (control)	Test statistic, Mann-Whitney <i>U</i> test
Examination/antennation	0.09 ± 0.04	0.00 ± 0.00	Z = -2.99, $P < 0.05$
Alarm/avoidance	0.40 ± 0.05	0.09 ± 0.05	Z = -2.70, $P < 0.05$
Aggression	0.18 ± 0.04	0.82 ± 0.07	Z = -3.14, $P < 0.05$

Values are mean (no. of occurrences per 10 s) ± SE, $n = 10$ for each combination.

at side base of mandibles; (3) length of head at side base of mandibles; (4) pronotum length; (5) pronotum width; (6) mesonotum width; (7) metanotum width; (8) hind tibial length; and (9) antennal length. We analyzed all soldier measurements using SPSS 11.0 discriminant analysis (SPSS 2002) to study which soldier castes were parasitized. Using the same software, the Student *t*-test also was conducted to compare the morphological variation between parasitized soldiers and healthy soldiers. The heads of parasitized soldiers ($n = 10$) were dissected to examine contents. Immature larvae (second-third stages; $n = 20$) and workers ($n = 10$) from each examined nest were randomly chosen and inspected for the presence of the dipteran parasitoid.

Insect Rearing. The termites were kept together with fungus-comb and major and minor workers until the fly larva pupated to ensure that the soldiers were fed. The parasitized soldiers were maintained in plastic storage boxes (320 by 250 by 130 mm) with moistened vermiculite (100% wt:vol) in an incubator at 28 ± 1°C (Incucell; MMM Medcenter Einrichtungen, München, Germany). When the parasitized soldiers became inactive and exhibited abnormally enlarged abdomens, this indicated that the fly larvae were about to pupate. The fly larval emergence process ($n = 5$) was video-recorded (Sony Digital Handycam 8; Tokyo, Japan). The larvae pupated in the vermiculite until emergence into adult flies under the condition as described above. The emerged flies were preserved in 70% alcohol and were sent to R.H.L. Disney (Cambridge University) for identification. Detailed descriptions on this fly were published previously (Disney et al. 2009).

Results

Survey of Dipteran Parasitoids. Thirteen of 17 mounds (77%) that were overgrown with grass contained parasitized termites, whereas 8 of 42 mounds (19%) that had been broken up previously for other experiments contained parasitized termites.

Behavioral Changes. Parasitized soldiers showed a significantly lower level of interspecific aggressiveness compared with healthy soldiers (Table 1). Alarm/avoidance behavior was the most frequent behavior observed (Kruskal-Wallis test, $\chi^2 = 12.107$, $P < 0.05$). In addition, three typical behaviors were observed. (1) In most instances, the parasitized soldiers avoided

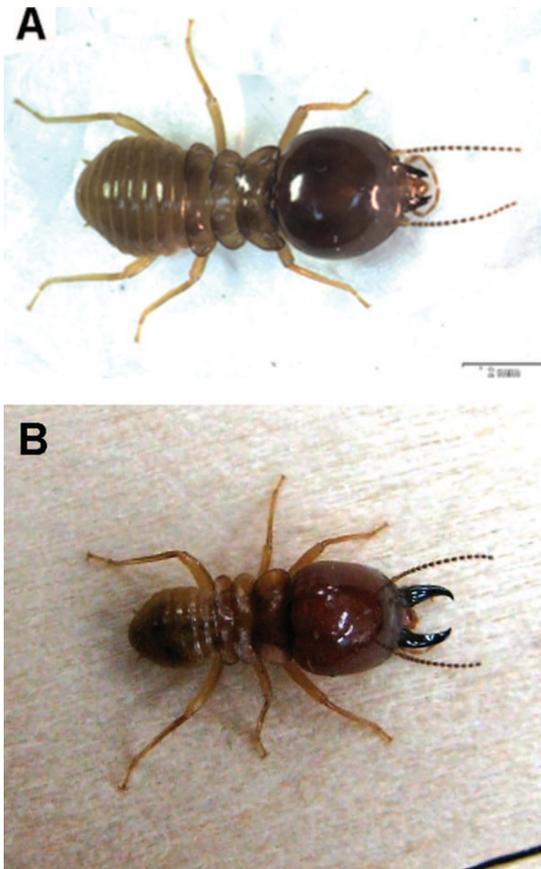


Fig. 1. *Macrotermes gilvus* soldiers. (A) Parasitized soldier. (B) Healthy soldier. (Online figure in color.)

or retreated from an opponent's attack on confrontation. (2) In only two cases did the parasitized individual perform jerking behavior when encountered with an alien termite. (3) The most aggressive behavior displayed by the parasitized soldiers was the opening of the mandibles. Total mortality (100%) of parasitized soldiers was the outcome of the encounters. Parasitized soldiers tended to congregate in one particular chamber of the termite mound (18 of 21 parasitized mounds) instead of the location where the healthy soldiers often found (i.e., fungus combs).

Morphological Changes. The parasitized soldier of *M. gilvus* (Fig. 1A) is quite distinct compared with the

healthy soldiers (Fig. 1B). An abnormally rounded head capsule and remarkably short mandibles are the characteristics of the parasitized soldiers. The mandible length is 0.89 ± 0.02 mm compared with 1.78 ± 0.05 and 1.32 ± 0.02 mm in healthy major and minor soldiers, respectively. Moreover, the parasitized soldier's head is significantly broader than that of a healthy soldier (Table 2). Additionally, the parasitized soldier possesses longer antennae (no. antennal segment = 17) but a shorter hind tibia compared with healthy specimens.

The first discriminant variables (Fig. 2), which accounted for 83% of the total variance (eigenvalue: 64.900), separated parasitized soldiers and major soldiers from minor soldiers and were most heavily weighted on antennal length, pronotum length, and mesonotum length. The second discriminant variables, which accounted for 6.5% of the total variance (eigenvalue: 2.834), isolated parasitized soldiers from major soldiers. This might suggest that only major soldiers are the targets of *M. mindeni* parasitism.

Fly larvae were found in the heads of immature larval instars ($n = 6$) (head width: 1.44–1.57 mm; pronotum width: 1.04–1.10 mm; antennal length: 2.42–2.58 mm; hind tibial length: 1.44–1.59 mm). Parasitized immature larval instars can be readily identified by a brown dot on the head capsule, but no morphological changes were observed. Parasitized presoldiers ($n = 15$) with a rounded head possess a pair of shortened soldier-like mandibles. Thus far, no workers have been found to be parasitized by *M. mindeni*.

Larval Emergence Process. Five video recordings on the larval emergence process were analyzed in this study. Only a single larva per host was observed. The fly larva developed in the termite soldier's head capsule and filled the whole capsule lumen. Once the fly larva had consumed the entire content of the termite soldier's head capsule, it was ready to pupate ≈ 1 wk later under laboratory conditions. During larval pre-emergence, the empty-headed parasitized soldier with an enlarged abdomen appeared to be capable of only moving slowly. A few hours later, the fly larva contracted intensively and applied sideways pressure to the intersegment membrane of soldier's abdomen, using spiracles to perforate the termite's abdominal wall. The process took ≈ 10 min to complete. Body fluid in the termite abdomen oozed out of the abdominal wall perforation.

Table 2. Mean \pm SE (range) of measurements of individual parasitized soldiers ($n = 20$) and healthy soldiers (major soldier, $n = 10$) of *M. gilvus*

Major soldier	Parasitized soldier	Healthy soldier	Test statistic
Maximum width of head	3.53 ± 0.03 (3.31–3.82)	3.17 ± 0.03 (3.05–3.34)	$t = 7.14$, $df = 28$, $P < 0.01$
Width of head at side base of mandibles	1.51 ± 0.02 (1.35–1.84)	1.74 ± 0.02 (1.64–1.85)	$t = -6.32$, $df = 28$, $P < 0.01$
Length of head at side base of mandibles	3.38 ± 0.03 (3.09–3.59)	3.43 ± 0.05 (3.23–3.65)	$T = -0.92$, $df = 28$, $P > 0.01$
Length of pronotum	1.20 ± 0.01 (1.08–1.32)	1.19 ± 0.03 (1.08–1.31)	$t = 0.63$, $df = 28$, $P > 0.01$
Width of pronotum	2.62 ± 0.03 (2.39–2.91)	2.60 ± 0.02 (2.49–2.73)	$t = 0.40$, $df = 28$, $P > 0.01$
Width of mesonotum	2.53 ± 0.03 (2.31–2.78)	2.45 ± 0.04 (2.31–2.67)	$t = 1.44$, $df = 28$, $P > 0.01$
Width of metanotum	2.75 ± 0.03 (2.41–3.02)	2.46 ± 0.04 (2.30–2.73)	$t = 5.42$, $df = 28$, $P > 0.01$
Length of hind tibia	2.42 ± 0.03 (1.97–2.73)	2.47 ± 0.03 (2.29–2.64)	$t = -8.52$, $df = 28$, $P < 0.01$
Length of antenna	3.13 ± 0.05 (2.87–3.84)	2.94 ± 0.05 (2.68–3.18)	$t = 7.97$, $d.f. = 28$, $P < 0.01$

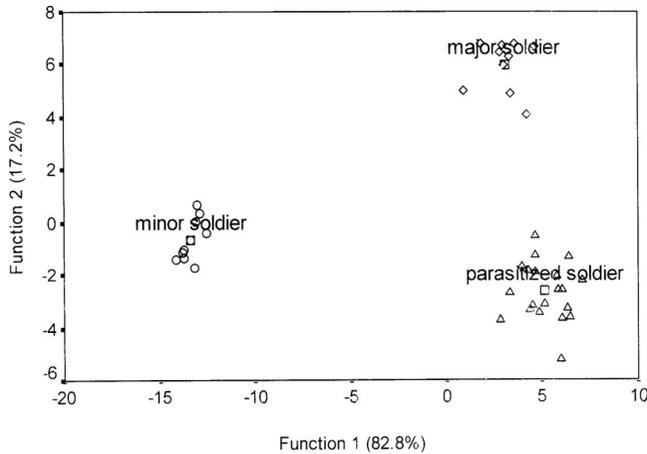


Fig. 2. Canonical discriminant functions of *M. gilvus* soldiers.

Fly pupae ($n = 23$) failed to pupate and eventually dried out under the laboratory conditions. Normally, they develop well in $\approx 90\%$ RH conditions in ≈ 14 d.

Discussion

The fly larva exerted a strong behavioral impact on *M. gilvus* soldiers. Our results are similar to those reported by Sze et al. (2008), who noted less aggressive behavior. The less aggressive behavior might be caused by their short and deformed mandibles, which made the parasitized soldiers less effective in fighting. This might take these parasitized soldiers out of a confrontation situation (e.g., nest defense), thus promoting better survival chances for the fly larva. During the encounters, the parasitized soldiers were unable to raise their head capsule and shied away when subjected to an external stimulus (e.g., when probed with a clean forceps). They usually congregated at one side of the container and are likely photophobic.

One of the most common behavioral changes caused by parasitoids is the changes in habitat preference of hosts by parasitoids (Brodeur and Boivin 2004). Parasitized hosts may move to elevated and exposed sites (Stamp 1981) or select more concealed microhabitat (Brodeur and McNeil 1989b). In most cases, we observed that the parasitized soldiers were isolated in a concealed empty chamber at the side of mound, where neither food resource (e.g., fungus comb) nor healthy soldiers and workers would be present. Such behaviors also have been reported for the Japanese beetle and masked chafer grubs (Roger et al. 2003), aphids (Brodeur and McNeil 1989a), and cabbage moth (Glouson 1997). This might be an adaptive strategy that facilitates parasitoid dispersal after emergence (Feener and Brown 1997) or provides protection against predation and environmental changes (Stamp 1981, Brodeur and McNeil 1992). In view of any benefit to the colonies, this behavior might reduce the risk of parasitism of other termite individuals in

any one colony (Feener and Brown 1997, Brodeur and Boivin 2004).

The morphology of parasitized soldiers shows a marked difference compared with healthy soldiers. The head capsule appears to be broader to provide room and allow the larval parasitoid to develop in a space-constrained environment. The parasitized soldier possesses long antennae with no additional antennal segments. Parasitized soldiers of *M. malaccensis* (Thapa 1977) and *M. carbonarius* (unpublished data) also were reported to have additional antennal segments.

Parasitoid oviposition decisions may be influenced by the quality of the host (Nofemela and Kfir 2007) and defensive behaviors of the host (Kouamé and Mackauer 1991). Host aggressive behavior generally increases with host age and size (Nofemela and Kfir 2007). Hence, insects in sedentary stages (e.g., eggs, larvae, and pupae) are prone to attack by parasitoids (Stireman et al. 2006) to ensure parasitoid survival (Harvey et al. 1996). As evident from our observation of the parasitized fourth larval instars (L4) of *M. gilvus*, the *M. mindeni* larva passes through at least three termite development stages—L4, major presoldier, and major soldier—before it is ready to pupate. Our results confirmed the speculation of Sze et al. (2008) that parasitization may begin in an earlier termite larval stage and ruled out the involvement of physical contact of the adult female fly with the mature host. Feener and Brown (1997) stated that dipteran larval parasitoids show varied development times. Some species have a long development time and kill the host soon after oviposition; some species develop rapidly after oviposition; and others develop in parallel with seasonal changes by entering diapause. From our results, we speculate that the larval *M. mindeni* has a long development time in the termite host's head capsule.

Sze et al. (2008) and Neoh and Lee (2009b) documented that the mature larvae of *V. fusciventris* left the host from the head and exited between abdominal

cerci using mouth hooks, and the fly larvae pupated outside the host's body. The host remained alive for another 1–2 d after larval emergence and died eventually because of traumatic perforation of the host's abdominal wall. This departure route clearly differs from what we observed in this study (i.e., pupating inside the host's body). In many cases of ant (Hymenoptera: Formicidae) parasitism by phorid flies [e.g., *Atta sexdens* L., Tonhasca et al. 2001; *Solenopsis invicta* (Buren), Consoli et al. 2001; and *Lasius niger* L., Maschwitz et al. 2008], the fly larvae pupate in the host.

The fly *M. mindeni* is a solitary parasitoid of *M. gilvus* soldiers. It is a new (and the third) species of the genus *Misotermes* (Diptera: Phoridae) found to parasitize *M. gilvus*. The first species found was *Misotermes exenterans* Schmitz in Java (Kalshoven 1938 and Schmitz 1938, cited in Disney et al. 2009) and the second was *Misotermes vicinus* Borgmeier in Thailand (Borgmeier 1967). Besides *Misotermes*, other phorid flies, such as *Palpiclavina kistneri* Disney (Disney and Kistner 1989, 1992, 1997) and *Megaselia scalaris* (Loew) and *Dicranopteron philotermes* Schmitz (Disney and Kistner 1990) were reportedly found in the nests of *M. gilvus*. *P. kistneri* was found laying eggs on termite nymphs. In more recent studies, larvae of the fly *V. fasciventris* were reported to be parasitoids of *Macrotermes* soldiers [e.g., *M. carbonarius*, Neoh and Lee 2009b; *Macrotermes barneyi* (Light), Sze et al. 2008; and *Macrotermes malaccensis* (Haviland), Kemner 1925, cited in Sze et al. 2008].

The mechanism on how the larval parasitoid of *M. mindeni* enters the host is unknown. Such information is difficult to obtain because of the cryptic nature of subterranean termites and the limited knowledge of the biology of the genus *Misotermes*. We hope that this documentation of parasitism of *M. gilvus* by a new phorid fly species will stimulate further investigation, particularly on:

- (1) The mechanisms by which the parasitoid gains access to the host. Based on our observations, the female fly may access breached mounds (USM) and physically contact the host. However, this scenario does not explain the parasitism phenomenon in most cases at the Bayan Lepas site (i.e., concealed mounds that were overgrown with grass). In addition, the fly may come into contact with the soldiers during the foraging activity of the termites.
- (2) How the parasitoid elicits an immune response from the host, especially when it spends a relatively long period of time in the host.
- (3) Accurately determining the larval stages at which the parasitism first occurs.

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