Effects of Disturbance and the Presence of Termite and other Invertebrate Carcasses at Feeding Sites on the Behavior of the Subterranean Termite *Microcerotermes crassus* (Blattodea: Termitidae)

by

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ABSTRACT

Ten factors which may affect the behavior of *Microcerotermes crassus* Snyder were evaluated in this study. The factors include: disturbance, crushed workers or soldiers (nestmates or non-nestmates), crushed Asian subterranean termites (*Coptotermes gestroi* [Wasmann]), crushed longlegged ants (*Anoplolepis gracilipes* (Smith)), crushed Ghost ants (*Tapinoma indicum* Forel), crushed millipedes (*Harphaphe* sp.) and crushed wood lice (*Porcellionides* sp.). The distribution of *M. crassus* was recorded between treated and untreated areas on day 1 and day 6 post-treatment. Observations show that disturbances or the presence of carcasses only deterred the termites temporarily. However, prolonged treatment with crushed *C. gestroi* showed that termites avoided the treated area even at 6 days post-treatment. Initially, *M. crassus* was probably deterred from the treated area temporarily because of the presence of *C. gestroi* carcasses. However, repeated treatments soon lead to fungi growth on the wood blocks and carcasses, rendering the area and the food unfit for the termites. Survival was also lowest in dishes treated with crushed *C. gestroi* which could be attributed to the presence of fungi. Termites consumed less wood in the dishes containing or treated with crushed conspecifics (workers or soldiers of nestmates and non-nestmates), or with *C. gestroi*. *M. crassus* either consumed the carcasses or buried them with sand.

Key Words: Termitidae, *Microcerotermes crassus*, disturbances, carcasses, behavior

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INTRODUCTION

Microcerotermes crassus Snyder is common in Peninsular Malaysia (Tho 1992). It builds mainly above-ground nests or arboreal nests in the lowlands of Peninsular Malaysia. *M. crassus* can also be readily found in and around rural dwellings and in the suburban areas (Tho 1992, Lee *et al.* 2007) and occurs often together with other pest termites in one building (Lee *et al.* 2007). *Coptotermes gestroi* is usually the dominant species and *M. crassus* is very likely to have encounters with it. Previous studies showed fierce attacks from both sides, resulting in heavy losses (Wong & Lee unpublished). *M. crassus* and *C. gestroi* would frequently attack each other. The feeding site where both of these species meet could be contaminated with cadavers.

Encounters between *M. crassus* with other termites (same or different species) and with other insects such as ants may result in fighting and subsequently carcasses may be left at feeding sites. Moreover, *M. crassus* may encounter other invertebrate carcasses such as millipedes and wood lice that can be found within their nests, at feeding sites around buildings, etc.

It is common to see behavioral reactions of healthy nestmates against diseased or dead individuals in social insects (Su 1982). When termites are exposed to soil treated with a slow-acting toxicant, dead termites that accumulate at the site of exposure will subsequently cause foraging termites to avoid that particular area. Termites could also have learned to avoid feeding in treated areas as a result of sub-lethal exposure to a slow-acting toxicant (Su & Scheffrahn 1991, Su *et al.* 1995). This behavior has been reported in *Coptotermes formosanus* tested with sulfluramid (Su & Scheffrahn 1991) and hydramethylnon (Su *et al.* 1982). However, Woodrow *et al.* (2008) suggested that a direct stimulus is not necessary to cause learned avoidance. Instead, contact with dead or moribund nestmates is enough to produce this behavior. Su (1982) termed this behavior as 'necrophobic behavior'.

Campora & Grace (2007) found that *C. formosanus* did not avoid borate-treated wood as a result of necrophobia or a learned response. Instead, the termites appeared to avoid the location of the toxic resource because of a decrease in amounts of trail pheromone (due to termite mortality) rather than the chemical treatment itself.

When termites interact with dead nestmates a range of behaviors are exhibited. It can begin with anti-feeding effects and ultimately, abandonment of a site and walling-off of dead termites and the source of mortality (Woodrow *et al.* 2008). Different termite species may react differently towards introduced disturbances and the responses vary within a species depending on the type of disturbance. In the extreme, termites may even abandon their nest temporarily or permanently (Noirot & Darlington 2000).

Here we hypothesize that the presence of carcasses (i.e. dead termites, ants, millipedes, etc.) at the food source will have a negative effect on the behavior of *M. crassus*. As part of our ongoing research into the biology and interactions between Malaysia's pest species of termites, we initiated this study to determine the effects of disturbance and the presence of termite and other invertebrate carcasses at feeding sites on the behavior of *M. crassus*.

MATERIALS AND METHODS

Termites

M. crassus was collected from the field within the vicinity of Universiti Sains Malaysia, Minden campus, Penang Island, Malaysia. Part of the nest was excavated to obtain the required number of termites. The nest portion was brought back to the laboratory and the termites separated out by lightly tapping on the nest carton. Then the termites were carefully isolated from nest and soil debris by using a piece of moistened and crumpled filter paper.

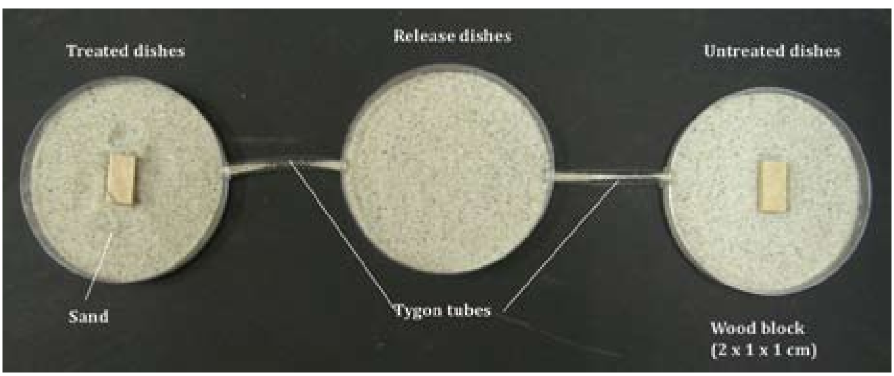

Fig. 1: Experimental set-up for the study on the effects of disturbance and the presence of termite and other invertebrate carcasses at feeding sites of *M. crassus.*

Assay

Three Petri dishes were connected to one another using tygon tubes measuring around 5 cm in length and 0.4 cm in diameter. Sieved sand (40 g- mesh size 4) was placed into each container and 8 ml of water were added to moisten the sand. One rubber wood (*Hevea brasiliensis*) block (2 cm x 1 cm x 1 cm) was placed in the middle of both the right and left Petri dishes (Fig. 1). The central Petri dish with moistened sand only was designated as the release dish, where 250 workers and 15 soldiers of *M. crassus* were introduced. The experimental set-up was kept in the dark (25.2 ± 0.2 °C, 56.3 ± 0.7 % RH) for one week. After this acclimatization period, one of the Petri dishes containing a rubber wood block was randomly chosen for treatment.

Table 1 lists the procedures carried out after the acclimatization period. Each treatment was repeated at weekly intervals two more times before the experiment was discontinued. The distribution of termites was ranked as follows: (0= no termites, 1= low termites [<20 individuals], 2= moderate number [20 – 50 individuals], 3= high number [>50 individuals]) on the 1st and 6th day post-treatment. At the same time, the floors of the dishes were scanned using a flatbed scanner (Canon CanoScan LiDE20, China Inc., China). On the 5th week, the set-up was dismantled and numbers of surviving termites were counted. The rubber wood blocks were washed and oven-dried at 50°C for 2 days before weighing to obtain the difference in wood loss between treated and untreated sections. Using the same colony, the experiment was replicated five times for each treatment.

Analysis

Termite distribution ranks were statistically analysed using the non-parametric Wilcoxon signed rank test. Wood consumption between wooden blocks in treated and untreated dishes was compared using the paired-t test at α=0.05. Termite survival (%) was transformed into arcsine values before being analysed using one-way ANOVA. Means were separated using Tukey HSD. All analyses were performed using Statistix® Version 7.0 (Analytical Software, Tallahassee, Florida).

RESULTS AND DISCUSSION

Termites approaching or moving away from a certain area following an induced disturbance form a complex distribution pattern (Hu *et al.* 2003).

Table 1: The procedures carried out on week 2, 3 and 4 of this study.

Factor	Treatment
Control	Nothing was done to all rubber wood blocks.
Wood disturbance	The rubber wood block (in treatment dishes) was removed and termites present on the wood were knocked back into the dish. Then, after 5 minutes, the block was placed back into its original location.
Crushed workers (nestmates)	The rubber wood block (in treatment dishes) was removed and used to crush 10 worker termites from the same colony in a Petri dish. The wood block with the crushed carcasses left on it was placed back into its original position.
Crushed soldiers (nestmates)	The rubber wood block (in treatment dishes) was removed and used to crush 5 soldier termites from the same colony in a Petri dish. The wood block with the crushed carcasses left on it was placed back into its original position.
Crushed *C. gestroi*	The rubber wood block (in treatment dishes) was removed and used to crush 10 *C. gestroi* worker termites collected from the field in a Petri dish. The wood block with the crushed carcasses left on it was placed back into its original position.
Crushed Yellow Crazy Ants (*A. gracilipes* (Smith))	The rubber wood block (in treatment dishes) was removed and used to crush 10 *A. gracilipes* from the ant culture in the laboratory in a Petri dish. The wood block with the crushed carcasses left on it was placed back into its original position.
Crushed Ghost Ants (*T. indicum* Forel)	The rubber wood block (in treatment dishes) removed and used to crush 20 *T. indicum* from the ant culture available in the laboratory in a Petri dish. The wood block with the crushed carcasses left on it was placed back into its original position.
Crushed workers (non-nestmates)	The rubber wood block (in treatment dishes) was removed and used to crush 10 worker termites from a different colony in a Petri dish. The wood block with the crushed carcasses left on it was placed back into its original position.
Crushed soldiers (non-nestmates)	The rubber wood block (in treatment dishes) was removed and used to crush 5 soldier termites from a different colony in a Petri dish. The wood block with the crushed carcasses left on it was placed back into its original position.
Crushed millipede (*Harphaphe* sp.)	The rubber wood block (in treatment dishes) was removed and used to crush 1 *Harphaphe* sp. collected from the field in a Petri dish. The wood block with the crushed carcasses left on it was placed back into its original position.
Crushed woodlice (*Porcellionides* sp.)	The rubber wood block (in treatment dishes) removed and used to crush 5 *Porcellionides* sp. collected from the field in a Petri dish. The wood block with the crushed carcasses left on it was placed back into its original position.

Our study showed that at day 1 post-treatment, *M. crassus* avoided the treated dishes. However, inspection at 6 days post-treatment showed that the termites had revisited the disturbed area. They were congregated around the wood blocks and feeding to an extent that would indicate that the termites were repelled only for a limited period after treatment.

Tunnel formations could be seen from the underside of all Petri dishes. Moreover, shelter tubes were also formed above the sand leading towards the rubber wood in both treated and untreated dishes. In some of the release dishes, shelter tubes and tunnels were made between the opposing exits.

Wood blocks with crushed workers and soldiers of *M. crassus* showed no traces of these termite carcasses after 6 days (except for the presence of a few head capsules of crushed soldiers). Most likely, the termites had consumed the carcasses.

M. crassus covered the dead carcasses of crushed *C. gestroi* (Fig. 2) and crushed *Tapinoma indicum* (Fig. 3) with sand. Removal of infected or dying termites from the colony or isolation/burying of termites can inhibit the spread of infection (Pearce 1997) or eliminate the source of contamination

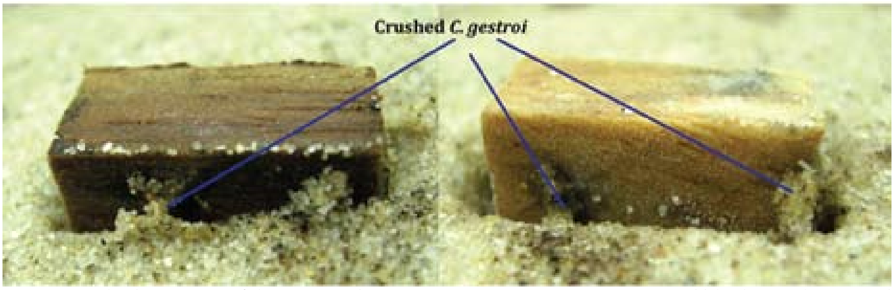

Fig. 2: Crushed carcasses of the Asian subterranean termite, *C. gestroi* on wood blocks partly covered with sand by *M. crassus*.

Fig. 3: Crushed carcasses of ghost Ants, *T. indicum,* covered within shelter tubes built with sand by *M. crassus*.

(Su 1982). Su *et al.* (1982) reported that foraging termites walled-off and avoided the area where large numbers of dead and decaying termites accumulated in soil treated with a slow-acting toxicant. *C. formosanus* was observed to bury dead termites in gallery walls as a means to avoid further contact (Su *et al.* 1982). It is also a means of preventing contamination of the carcasses with pathogens which could spread through a group or colony of termites (Pearce 1997). Therefore, regular feeding on the wood will prevent or reduce the spread of fungi. This is important because poisoned or dead termites will often become repellent after a certain time (Pearce 1997). A study carried out by Chouvenc *et al.* (2005) showed that as soon as some of the alates of *Pseudacanthotermes spiniger* died, necrophobic behavior could be observed. The alates were observed to groom and cover the cadavers with saliva before they were buried with sand and soil, thus physically isolating the cadavers.

Observations showed that fungi were present on the wood blocks treated with crushed *C. gestroi* and crushed *T. indicum* as well as on the carcasses. If termites are present, they can keep things in check up to a point, if not, fungi can take over. Fungi can grow on cadavers and often other types of fungi such as bluestains and soft-rot fungi can grow on wood (Becker 1969). Lefevre-Rouland (2000) reported that certain fungi can act as parasites of termites and the mycelium and spores of certain fungi can be harmful to termites when consumed. Some of the fungi on cadavers can also produce potent toxins (e.g. *Aspergillus* fungi) once they sporulate (Becker 1969). A*spergillus flavus* was found to be toxic to *C. formosanus* and as the fungi concentration increases, mortality of termites also increased (Jayasimha 2006).

The presence of fungi could be due to specific circumstances. In our study, *M. crassus* was first deterred by the carcasses of *C. gestroi* at 1 day post-treatment, but on the 6th day, the termites were back in the treated area. However, at week 4 (3rd treatment), fungi had covered the surfaces of the rubber wood blocks which were placed in the dishes treated with crushed *C. gestroi*. The numbers of *M. crassus* in the treated dishes were reduced. The termites could have been deterred by *C. gestroi* carcasses long enough for fungi to readily develop on the wood blocks. Abandonment of wood blocks treated with carcasses can trigger fungi to thrive and spread (Pearce 1997). The presence of the fungi then renders the wood less suitable for feeding, especially since the blocks were kept on a moist matrix. According to Pearce (1997), food

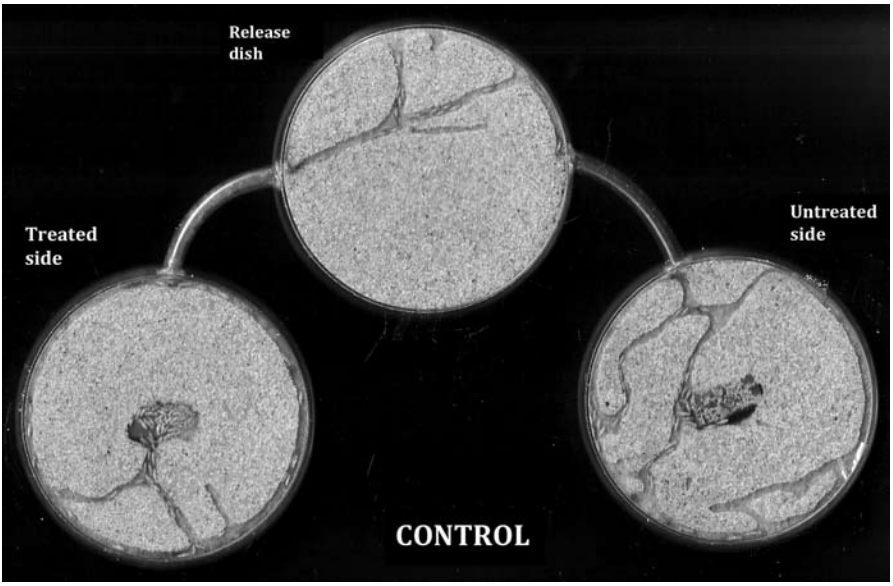

Fig. 4: Distribution of *M. crassus* in each interconnected Petri dish in control at the end of week 4.

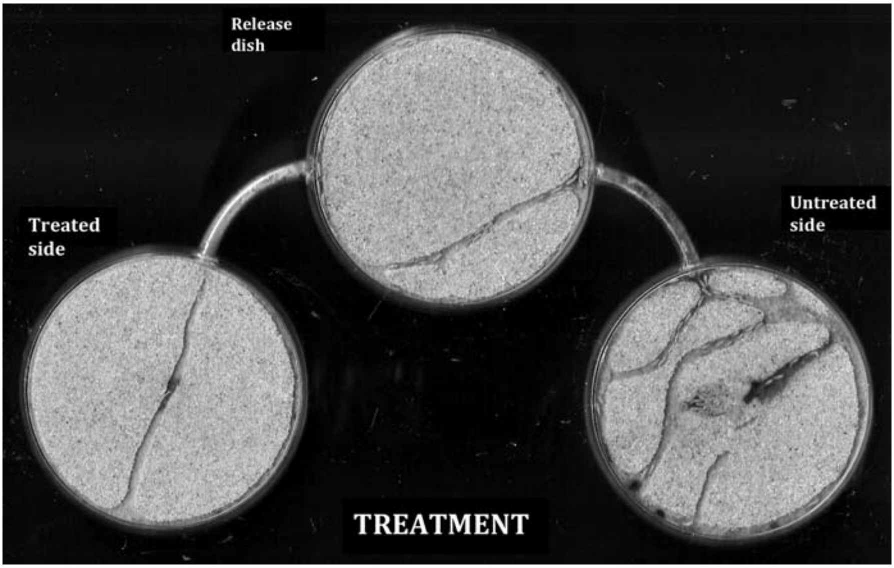

Fig. 5: Distribution of *M. crassus* subjected to treatment performed on the left Petri dish which showed less presence of termites at the end of week 4.

sources under humid conditions can be colonised and attacked by fungi. Contamination of a food source with microorganisms can deter termites and thus reduce termite activities within the fungus-infected area. There is primary deterrence from *C. gestroi*, which in turn leads to secondary changes of the food source (fungal growth). Hence, two impacts come together to contribute to the detriment of *M. crassus*.

Fungi were also present on wooden blocks with crushed *T. indicum* but fungal presence/growth was less extensive compared to wood blocks treated with crushed *C. gestroi*. In this study, *M. crassus* was able to withstand the fungi present in dishes treated with *T. indicum*.

Figs. 4 to 6 show the distribution patterns of *M. crassus* between the controls and some of the treatments. In the controls, termites were spread out evenly across all three dishes (Fig. 4). But depending on the type of treatment, termites were either absent from the treated area (Fig. 5) or treatment had limited to no impact on termite distribution (Fig. 6).

After the initiation of treatments in weeks 2, 3 and 4, the number of termites visible underneath the treatment dishes was significantly lower compared to untreated dishes ($p<0.05$) for crushed workers and soldiers (nestmates or

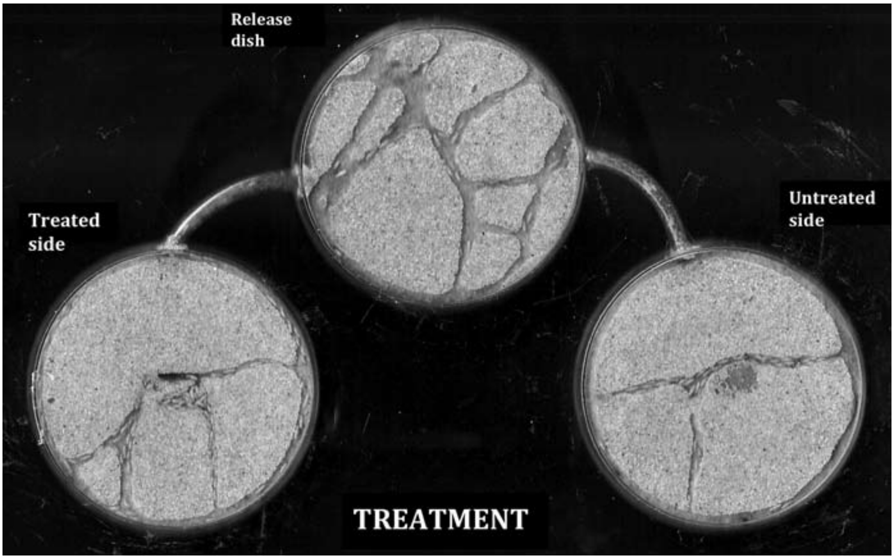

Fig. 6: Distribution of *M. crassus* subjected to treatment performed on the left Petri dish showing presence of termites in all dishes at a rather equal amount at the end of week 4.

non-nestmates), or crushed *C. gestroi* at day 1 post-treatment. The soldier frontal glands contain various compounds which might elicit the responses in *M. crassus* workers described here when they encountered crushed soldier heads. Reinhart & Clement (2002) found that the alarm reactions of several *Reticulitermes* spp. were generated by crushed soldier heads. Schwinghammer & Houseman (2006) reported that the alarm responses by *Reticulitermes flavipes* usually consist of an immediate partial evacuation. A movement back into the site follows and eventually more termites are present in the area after the alarm than before.

Treatment with crushed *Anoplolepis gracilipes*, *T. indicum*, *Harphaphe* sp., and *Porcellionides* sp. or disturbance of the food source did not deter *M. crassus*. Numbers of termites present in the treated areas and at the food sources was not significantly different from the untreated areas ($p>0.05$) at any point of the experimental period.

By day 6 post-treatment for weeks 2, 3 and 4 (Figs. 7, 8 and 9), termite numbers in most treated dishes revealed no significant difference when compared to the number of termites in the untreated dishes ($p>0.05$). Although

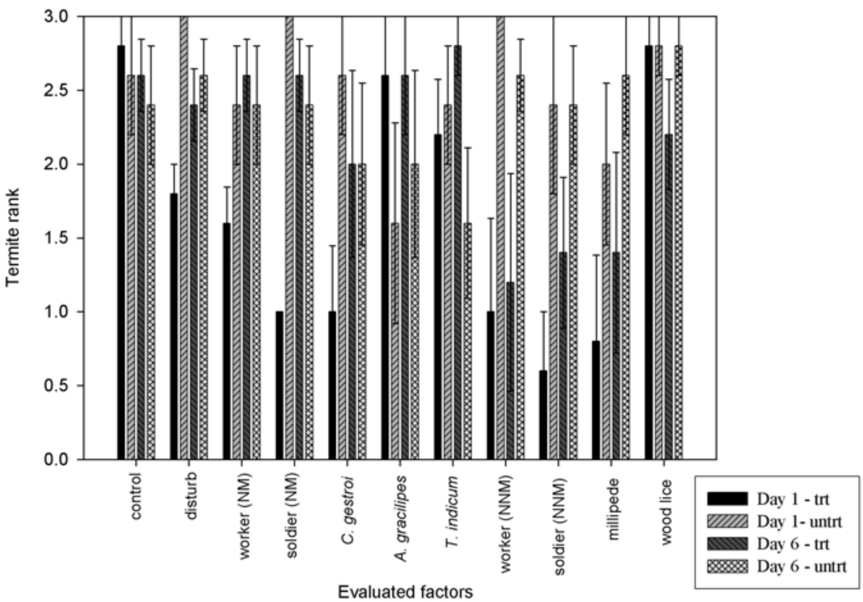

Fig. 7: Termite number in dishes containing treated and untreated woods on day 1 and day 6 of week 2.

termite numbers were not significantly different between the treated and untreated dishes by day 6 post-treatment at week 2 and 3 for dishes treated with crushed *C. gestroi*, termite numbers were significantly different ($p<0.05$) between treated and untreated dishes by day 6 post-treatment at week 4.

This shows that some of the factors evaluated only have a temporary effect on the behavior of *M. crassus* and termites will usually return to the treated sites within one or a couple of days after the effects of the treatments have lessened. In workers and soldiers of *R. flavipes* and *C. formosanus*, various vibrational frequencies were found to cause them to withdraw from the source of vibration (Hu *et al.* 2003). However, the alarm responses were brief. In our study, only crushed *C. gestroi* appeared to deter termites after a prolonged period of treatments. Other factors could be involved to explain prolonged avoidance of a site with cadavers of *C. gestroi* such as specific compounds in the cadaver which identify them as those of the main competitor to *M. crassus,* or anti-feedants.

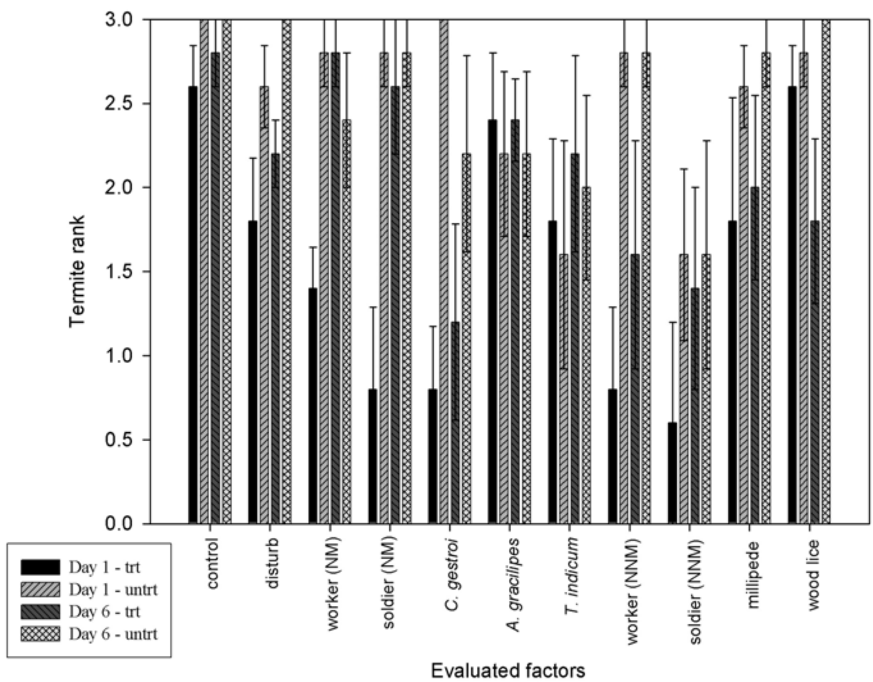

Fig. 8: Termite number in dishes containing treated and untreated woods on day 1 and day 6 of week 3.

In laboratory trials, the feeding activity of both *C. formosanus* and *R. flavipes* was significantly reduced on food sources that were contaminated with dead or moribund termites (Woodrow *et al.* 2008). This corresponds well with the results (Table 2) of our study, where wood consumption of *M. crassus* was significantly affected by all the treatments involving termites ($p<0.05$). The other factors evaluated showed no significant differences in wood consumption ($p>0.05$).

Fig. 10 shows the mean percentage of surviving termites. The survival rate was relatively high in dishes treated with crushed nestmate workers (83.8%), nestmate soldiers (76.3%), non-nestmate workers (76.2%), non-nestmate soldiers (73.4%), *A. gracilipes* (81.8%), *T. indicum* (77.3%) and dishes containing wooden blocks that were disturbed (77.8%). Groups exposed to crushed *C. gestroi* experienced the lowest survival (55%) of all termite and ant treatments $p<0.05$), with the exception of crushed *Harphaphe* sp. and *Porcellionides* sp. ($p>0.05$).

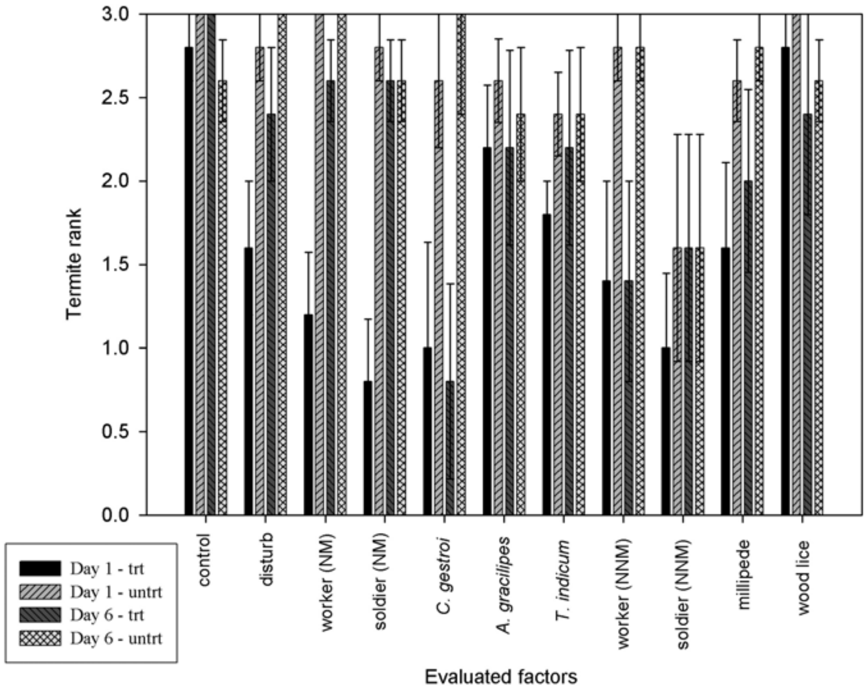

Fig. 9: Termite number (distribution) treated and untreated dishes on day 1 and day 6 of week 4.

Table 2: Wood consumption (mean ± S.E.M.) of *M. crassus* in treated and untreated dishes.

Treatments	Wood consumption (gm) (mean ± S.E.M.) Treated dish	Untreated dish
Control	0.1697±0.0181[a]	0.2053±0.0153[a]
Disturbance	0.1588±0.0090[a]	0.2281±0.0139[a]
Crushed workers (nestmates)	0.0745±0.0104[a]	0.2073±0.0342[b]
Crushed soldiers (nestmates)	0.0542±0.0135[a]	0.1806±0.0108[b]
Crushed workers (non-nestmates)	0.1078±0.0018[a]	0.2052±0.0160[b]
Crushed soldiers (non-nestmates)	0.0749±0.0060[a]	0.1783±0.0082[b]
Crushed *Coptotermes gestroi*	0.0962±0.0090[a]	0.1828±0.0278[b]
Crushed *Anoplolepis gracilipes*	0.1561±0.0154[a]	0.2479±0.0409[a]
Crushed *Tapinoma indicum*	0.1733±0.0196[a]	0.1881±0.0167[a]
Crushed millipede	0.1846±0.0269[a]	0.1921±0.0142[a]
Crushed wood lice	0.1194±0.0170[a]	0.1321±0.0175[a]

[a] Means followed by different letters within the same column are significantly different at α=0.05 (paired t-test)

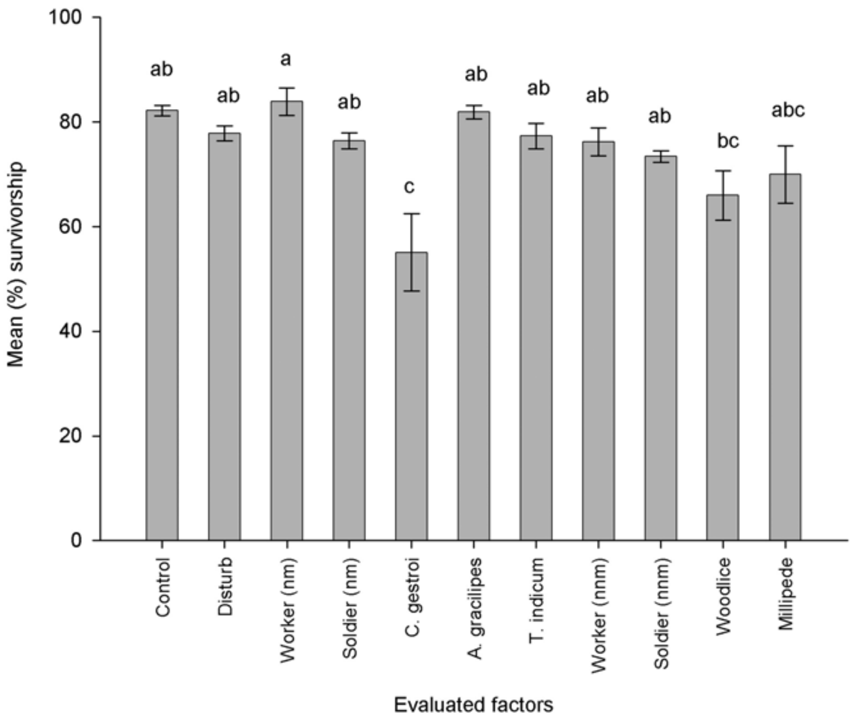

Fig. 10: Survival (%) of *M. crassus* subjected to various treatments (disturbances) at the end of the experimental period (Tukey HSD, $p<0.05$)

Our previous research has given a deeper insight into intra- and interspecific interactions in the pest species community around buildings and in other habitats where those species co-occur. When *M. crassus* and *C. gestroi* came in contact with each other, intense fighting erupts, resulting in the death of many of the participants (Wong & Lee unpublished). However, such confrontations have a more lasting impact on *M. crassus*. The higher mortality of *M. crassus* recorded from dishes treated with crushed *C. gestroi* could have the following cause: *M. crassus* stayed away from dishes treated with *C. gestroi* for longer periods than for any other treatment. *C. gestroi* cadavers were also neither consumed nor walled in. Hence, mould and wood-colonising fungi had longer periods of unhindered growth and development. By the time *M. crassus* returned to the dishes it had to confront a more adverse environment with more significant microbial presence than in all other scenarios presented to termites in this study, probably resulting in higher mortality of *M. crassus* workers.

Thus, the dominance of *C. gestroi* over *M. crassus* and possibly other subterranean species of termite is achieved by a combination of greater aggressiveness of *C. gestroi*, longer-term avoidance of confrontation sites by the more timid species, and in consequence rendering sites of such encounters unsuitable for future use through unchecked microbial growth.

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REFERENCES

Becker, G., H. K. Frank, & M. Lenz. 1969. Die giftwirkung von *Aspergillus flavus*-stamen auf termiten in beziehung zu ihrem aflatoxin-gehalt. (The toxicity of *Aspergillus flavus*-strains on termites in relation to their aflatoxin content.) Z. ang. Zool. 56: 451-464 (Germ., Engl. sum.).

Campora, C. E., & J. K. Grace. 2007. Foraging behavior of the Formosan subterranean termite (Isoptera: Rhinotermitidae) in response to borate treated wood. International Research Group on Wood Preservation. Stockholm, Sweden. IRG document No. IRG/WP 01-10605. 13 pp.

Chouvenc, T., A. Robert, E. Se´mon, & C. Bordereau. 2005. Necrophobic behavior in termites induced by chemoreception. In: ABSTRACTS. List of Abstracts from the Sixteenth Annual Meeting of the European Chemoreception Research Organisation. Chemical Senses 30: E1–E64.

Hu, X. P., A. G. Appel, & J. F. A. Traniello. 2003. Behavioral response of two subterranean termites (Isoptera: Rhinotermitidae) to vibrational stimuli. J. Insect Behav. 16: 703-715.

Jayasimha, P. 2006. Interactions between Formosan subterranean termites, brown rot fungus (*Gloeophyllum trabeum*) and some of the fungi present on the termite integument and gut. M.S. dissertation. Louisiana State University and Agricultural and Mechanical College.

Lee, C. Y., C. Vongkaluang, & M. Lenz. 2007. Challenges to subterranean termite management of multi-genera faunas in South East Asia and Australia. Sociobiology 50: 213-221.

Lefevre-Rouland, C. 2000. Symbiosis with fungi. pp. 289-306. In: Abe, T., D. E. Bignell and M. Haigashi (eds) Termites: Evolution, Sociality, Symbioses and Ecology. Kluwer Academic Publishers, Boston, MA.

Noirot, C. H., & J. P. E. C. Darlington. 2000. Termite nests: architecture, regulation and defence. In: Abe, T., D. E. Bignell and M. Haigashi (eds) Termites: Evolution, Sociality, Symbioses and Ecology. Kluwer Academic Publishers, Boston, MA. Pp. 121-137.

Pearce, M. J. 1997. Termites: Biology and Pest Management. CAB International.

Reinhart, J., & J. –L. Clement. 2002. Alarm reaction of European *Reticulitermes* termites to soldier head capsule volatiles (Isoptera: Rhinotermitidae). J. Insect Behav. 15: 95-107

Schwinghammer, M. A., & R. M. Houseman. 2006. Response of *Reticulitermes flavipes* (Isoptera: Rhinotermitidae) to disturbance in laboratory arenas at different temperatures and soldier proportions. J. Econ. Entomol. 99: 462-468.

Su, N. Y. 1982. An ethological approach to the remedial control of the Formosan subterranean termite, *Coptotermes formosanus* Shiraki. Ph.D Dissertation, University of Hawaii.

Su, N. Y., M. Tamashiro, J. R. Yates, & M. I. Haverty 1982. Effect on behavior on the evaluation of insecticides for the prevention of or remedial control of the Formosan subterranean termite. J. Econ. Entomol. 75: 188-193.

Su, N. Y. & R. H. Scheffrahn. 1991. Laboratory evaluation of two slow-acting toxicants against Formosan subterranean termite (Isoptera: Rhinotermitidae). J. Econ. Entomol. 84: 170–175.

Su, N. Y., R. H. Scheffrahn, & P. M. Ban. 1995. Effects of sulfluramid-treated bait blocks on field colonies of the Formosan subterranean termite (Isoptera: Rhinotermitidae). J. Econ. Entomol. 88: 1343-1348.

Tho, Y. P. 1992. Termites of Peninsular Malaysia. Forest Research Institute Malaysia, Kepong, Kuala Lumpur.

Woodrow, R. J., T. G. Shelton, R. J. Oshiro, J. K. Grace & T. L. Wagner. 2008. Effects of disturbance-induced trauma on foraging behavior by subterranean termites (Isoptera: Rhinotermitidae). Sociobiology 52: 107-156.