Intra- and Interspecific Agonistic Behavior of the Subterranean Termite *Microcerotermes crassus* (Isoptera: Termitidae)

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ABSTRACT The aim of our study was to investigate the intra- and interspecific agonistic behaviors exhibited by the worker and soldier castes of the subterranean termite *Microcerotermes crassus* Snyder (Isoptera: Termitidae). Aggression between *M. crassus* colonies from different field locations and also against three termite species—*Coptotermes gestroi* (Wasmann), *Globitermes sulphureus* Haviland, and *Odontotermes* sp.—were observed in the laboratory. Termite responses were tested in paired combination of castes (soldiers versus soldiers, soldiers versus workers, and workers versus workers) consisting of 10 individuals each. Significant agonistic behaviors were observed only in encounters between pairings of different termite species. *M. crassus* was aggressive toward individuals from different species but not toward individuals from different *M. crassus* colonies. Mortality of *M. crassus* reached 100% in most of the interspecific encounters. However, no or low mortality was recorded in the intraspecific pairings.

KEY WORDS *Microcerotermes crassus*, intraspecific, interspecific, agonism, survival

Microcerotermes crassus Snyder (Isoptera: Termitidae) can be found in Southeast Asia and is especially common in peninsular Malaysia (Tho 1992). Although its nesting habit range from subterranean to arboreal (Takematsu et al. 2003), in the lowlands of peninsular Malaysia it builds nests mainly above ground or on trees. Termitidae is the largest termite family containing three-fourths of the known termite species (Krishna 1969).

M. crassus can be readily found in and around rural dwellings and in suburbia (Tho 1992, Lee et al. 2007). It often occurs concurrently with other pest termites in buildings (Lee et al. 2007). Although baiting helps to reduce or eliminate populations of rhinotermitids [e.g., *Coptotermes gestroi* (Wasmann)], other species normally considered as secondary pest species or nonpest species can enter buildings and pose a threat to the structure upon the primary species is eliminated (Lee 2002a,b; Kirton and Azmi 2005). In addition, it is common to find several termite species inhabiting or infesting a structure in peninsular Malaysia. Thus, the chance of different termite species encountering one another under natural condition is not uncommon.

When termites interact with termites of a different colony or species, a variety of agonistic behaviors can occur, ranging from no aggression to fierce combat (Su and Haverty 1991). We attempted to determine the aggressiveness of both worker and soldier castes of *M. crassus* and to ascertain the frequency of the various agonistic behaviors exhibited by *M. crassus*. Therefore, as part of our ongoing research into the biology of pest termite species of Malaysia, intraspecific interactions between *M. crassus* from different colonies and interspecific interactions between *M. crassus* and other pest species were studied.

Materials and Methods

Termite Collections. *Intraspecific Study. M. crassus* was collected from four locations: Universiti Sains Malaysia (Minden Campus, Penang Island, Malaysia), Muka Head (Penang, Malaysia), Balik Pulau (Penang, Malaysia), and Padang Serai (Kedah, Malaysia). Part of a given nest was excavated, broken off, and transported to the laboratory. Termites were gently tapped out of the nest carton and carefully isolated from soil debris with a piece of moistened and crumpled filter paper. Termites from each colony were maintained separately in a plastic container lined with moistened filter paper. Individuals were tested within a day after being collected from the field.

Interspecific Study. Three different termite species were tested against *M. crassus*, namely, *C. gestroi*, *Globitermes sulphureus* (Haviland), and *Odontotermes* sp. All termite species were collected from the field from within or in the vicinity of Universiti Sains Malaysia, Minden Campus, Penang Island. *C. gestroi* was collected from an in-ground monitoring station on Minden Campus. Using techniques described by Tamashiro et al. (1973), termites collected in the field were

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separated from soil debris in the laboratory. *G. sulphureus* was collected by excavating part of the mound and taking a section of it to the laboratory for separation, as described earlier for *M. crassus. Odontotermes* sp. was obtained by collecting foraging termites under dead branches or dried leaves on the forest floor. *Odontotermes* sp. together with any dead branches and dried leaves were gathered and brought back to the laboratory for separation. Each termite species was maintained separately in a plastic container lined with moist filter paper. Individuals were tested within a day after being collected from the field.

Assays. *Intraspecific Agonistic Study.* A filter paper disc (≈9 cm in diameter) moistened with distilled water was placed in a 9-cm-diameter petri dish, which served as the test arena. To separate the two groups of test termites, a clear plastic sheet was placed in the middle of the petri dish and acted as a partition (Fig. 1). This measure prevented contact before the start of the test.

M. crassus colonies were tested against each other in the following pairwise tests (workers versus workers, soldiers versus workers, and soldiers versus soldiers). All castes were paired in a 1:1 ratio (ten individuals (workers or soldiers) from each colony). Termites introduced into the test arena were left to acclimatize in their respective half for 10 min before removal of the plastic barrier. Once the plastic sheet was removed, events in the arena were recorded on video for 5 min. Each combination was tested five times, using a new arena each time. After the 5-min observation period, dishes were covered with lids and placed in the dark at room temperatures (25 ± 1.5°C and 56.3 ± 0.7% RH) for 24 h before the number of survivors was recorded.

In our bioassay, stained and unstained termites were used to differentiate between individuals from the opposing *M. crassus* colonies. Unstained termites were exposed to filter paper saturated with distilled water only. Stained termites were obtained by using the water-soluble, reliable, and widely used Nile Blue A (Fluka Chemika, Buchs, Switzerland) and Neutral Red (Sigma, St. Louis, MO) dyes. The dyes were used for the fast-marking method described by Evans (2000). Filter papers were dipped directly into dye solutions of either 0.5% Nile Blue A or 0.5% Neutral Red and allowed to become saturated. Thirsty termites that were previously exposed to the air for 1 h were placed on the stained filter paper and left for 3 d. Su et al. (1988) reported that dyes at proper concentrations and exposure times do not cause significant mortality.

Interspecific Agonistic Study. M. crassus was tested against *C. gestroi*, *G. sulphureus*, and *Odontotermes* sp. in pairwise tests (soldiers versus soldiers, soldiers versus workers, and workers versus workers) to examine interspecific agonistic behavior. The methods used were the same as those described above for the intraspecific aggression experiments, except that there was no need to mark termites with dye because each species was easily recognizable.

Data Analysis. Survival of termites in the different pairwise tests (intraspecific and interspecific studies) was analyzed using a paired *t*-test at $\alpha = 0.05$. Frequency for each aggression level was calculated before being subjected to Kruskal–Wallis test ($P < 0.05$). All analyses were performed using Statistix version 7.0 (Analytical Software, Tallahassee, FL).

Behaviors exhibited by *M. crassus* toward members of other *M. crassus* colonies and toward the three different termite species were noted for their rate of occurrence (Table 1). In both the intra- and interspecific studies, the behavior at first encounter and the behavior for the following 5 min were recorded. The mean frequency was then calculated to determine the aggression levels of *M. crassus* in interspecific encounters: 0, no aggression (NA; antennation); 1, less aggression (LA; jerking, avoidance, chasing/escaping); and 2, aggressive (A; attacks, defecation, grappling, biting). The competitiveness of *M. crassus* to be killed in these interactions by the opponent was classified into five levels based on the mean percentage of survival: 0%, not competitive (NC);

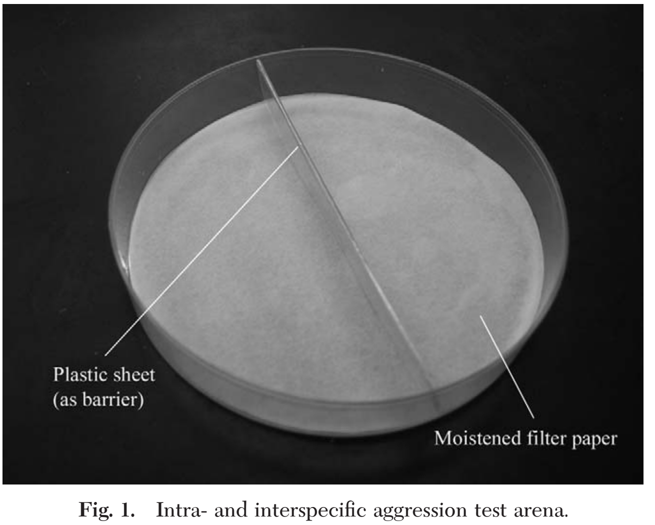

Fig. 1. Intra- and interspecific aggression test arena.

Table 1. List of different interaction behaviors (modified after Jmhasly and Leuthold 1999 and Adams 1991)

Behavior	Remarks
Examination	
Antennation	Contact between antenna/antenna or antenna/body
Alarm/Avoidance	
Jerking	Moving body up and down very quickly
Avoidance	Rapid reorientation and increase in walking rate
Chasing/escaping	Chasing and/or being chased
Aggression	
Attacks	Rapid lunge forward and attempts to bite the opponent
Defecation	Deposition of a droplet of anal fluid on or near the intruder
Grappling	Seize, hold, and drag one another with mandibles
Biting	Strong bites usually piercing the opponent's exoskeleton

>0–<25%, less competitive (LC); 25–<50%, moderately competitive (MC); 50–<75%, competitive (C); and 75–<100%, very competitive (VC).

Results and Discussion

Intraspecific Agonistic Study. Pairings from particular combinations will not necessarily result in aggressive encounters (Thorne and Haverty 1991). In our study, we found no evidence of aggression between any of the intraspecific pairings of *M. crassus,* although the colonies came from widely disparate area (distances between the four colonies ranged from 7.5 to 35.0 km). Husseneder and Grace (2001b) suggested the use of DNA fingerprinting to determine whether colony fusion exists or not in the field. It is likely that colonies which do not exhibit agonistic behavior would interact freely at foraging sites in the field (Cornelius and Obsrink 2003).

Very low or zero mortality was recorded in this study between the caste combinations of *M. crassus* from the different colonies. *Zootermopsis nevadensis* subsp. *nevadensis, Z. nevadensis* subsp. *nuttingi* (Haverty and Thorne 1989), *Macrotermes subhyalinus* (Rambur), and *M. bellicosus* (Smeathman) (Jmhasly and Leuthold 1999) collected from geographically disparate areas also did not exhibit any apparent intraspecific aggression. Genetic homogeneity has often been applied to explain the lack of agonism between termites collected from different location sites. This phenomenon has been reported in the populations of *Coptotermes formosanus* Shiraki in Florida (Korman and Parshley 1991) and Hawaii (Strong and Grace 1993, Broughton and Grace 1994). Nevertheless, Su and Haverty (1991) reported that not all colony pairs of *C. formosanus* from Hawaii showed agonism, whereas those from Florida did not show any agonism toward each other. This shows that geographical distance was not correlated with agonism (Su and Haverty 1991, Shelton and Grace 1997).

Generally, our results showed that encounters between different colonies of *M. crassus* were passive. Passive encounters are defined by Thorne and Haverty (1991) as antennation/mutual grooming or greeting with no apparent aggression. In this scenario, each individual from different colonies moves until there was contact. The interaction usually begins with antennal inspection of the opponent. However, in our study throughout the entire experimental period, limited occurrences of antennation or mutual grooming were observed. Termite species that do not show aggression between intraspecific colonies include *Amitermes beaumonti* Banks and *Armitermes chagresi* Snyder (Thorne 1982), *C. formosanus* (Delaplane 1991), *R. flavipes* (Grace 1996, Polizzi and Forschler 1998, Bulmer and Traniello 2002), and *Macrotermes michaelseni* (Sjöstedt) (Schuurman and Dangerfield 1995).

Fletcher and Michener (1987) indicated that many social insects can distinguish between kin and nonkin. It was suggested that physical and chemical components (cuticular components, exudates, volatiles, and behavioral and tactile differences) influences recognition cues (Su and Haverty 1991). In the kin recognition system, more than one cue was probably required and aggression may not occur if all cues are not present (Shelton and Grace 1997). Even with the presence of genetic diversity (Husseneder and Grace 2001a) and variation in chemical and environmental cues (Haverty et al. 1996), it does not necessarily confirm that nestmate recognition is visible.

Termites also display immediate and overt recognition behavior in intraspecific aggressions (Thorne 1982). Agonistic interactions between termites from different colonies have been described for several termite species in the field or laboratory, including *Heterotermes aureus* (Snyder) (Jones 1990, Binder 1988), *Hodotermes mossambicus* (Hagen) and *Trinervitermes trinervoides* (Sjöstedt) (Nel 1968), *Coptotermes acinaciformis* (Frogatt) (Howick and Creffield 1980), and *Microtermes* sp. nr. *albopartitus* (Sjöstedt), *Microtermes najdensis* Harris, and laboratory-reared colonies of *M.* sp. nr. *lepidus* Sjöstedt (Pearce et al. 1990). Thorne (1982) and Thorne and Haverty (1991) stated that the degree of intensity and the outcome of agonistic encounters vary among the species, colonies, and castes involved.

Of those termites that died during the experiment, their carcasses showed no signs of excision of appendages, which indicates that they were not attacked. The few deaths recorded might have been due to injuries resulting from our handling of the termites.

Interspecific Agonistic Study. Although no aggression between intraspecific pairings was observed, most of the interspecific pairings resulted in the displays of aggression of a certain level, both by the worker and soldier castes of *M. crassus* (Fig. 2).

All levels of aggressiveness were displayed at a similar frequency when *M. crassus* workers encountered both castes of *C. gestroi* as well as the workers of *Odontotermes* sp. Both castes of *M. crassus* exhibited behaviors that were less aggressive toward *G. sulphureus* workers. This phenomenon also was recorded for

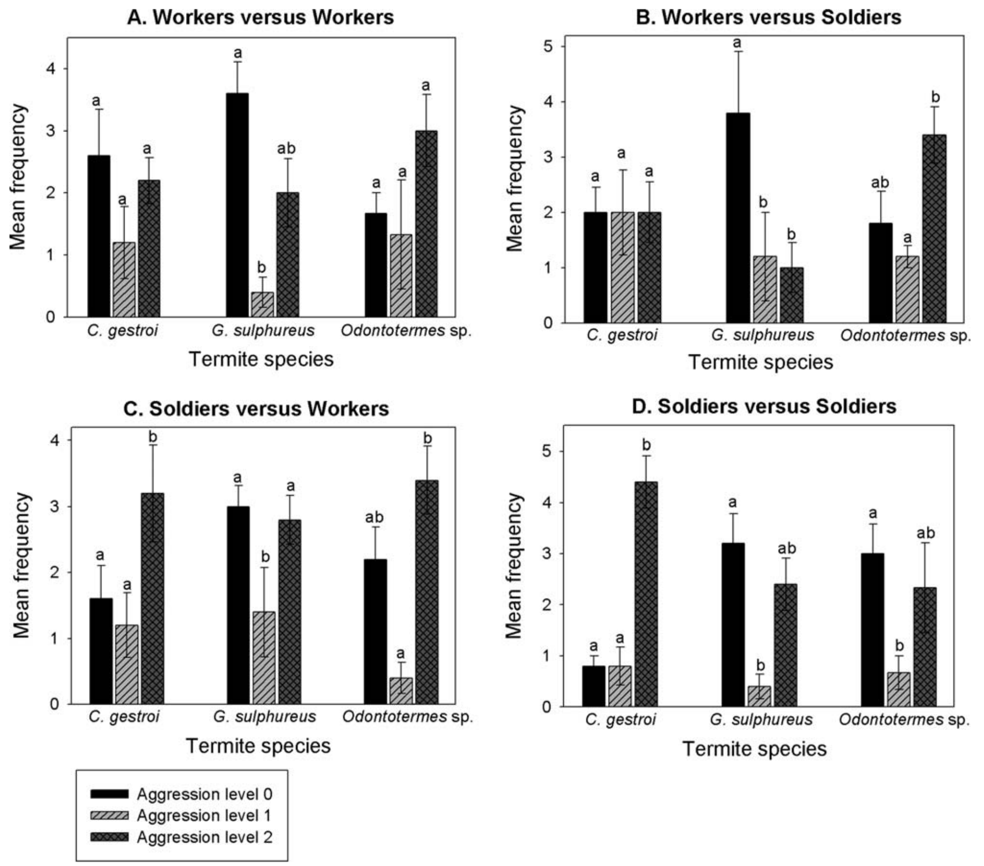

Fig. 2. Mean frequency of different aggression level (mean ± SEM) exhibited by *M. crassus* of various caste combinations toward other termite species over a period of 5 min ($P < 0.05$; Kruskal–Wallis).

M. crassus soldiers toward the soldiers of both *G. sulphureus* and *Odontotermes* sp.

M. crassus exhibited significantly more aggressiveness toward both castes of *C. gestroi.* When *M. crassus* encountered soldiers of *Odontotermes* sp., a significantly higher frequency of aggressiveness was displayed. Besides that, *M. crassus* soldiers also displayed a significantly higher frequency of aggressiveness when they encountered *Odontotermes* sp. workers.

Most of the behaviors exhibited by *M. crassus* workers toward soldiers of *G. sulphureus* were not aggressive. This shows that in some cases, the aggression level of *M. crassus* can be of similar frequency, whereas others can differ. Therefore, the aggressiveness of *M. crassus* tends to vary depending on the opponent species and caste.

Figure 3 shows the different types of behavior exhibited by both castes of *M. crassus* when they came across termites of a different species and caste. The most frequent type of behavior by *M. crassus* soldiers when tested against workers of other termite species was antennation (Fig. 3C). Antennation behavior was significantly more frequent between the soldiers of *M. crassus* and the workers of *C. gestroi* ($P < 0.05$). Similar frequency of antennation was recorded in worker–worker interaction and soldier-soldier interaction ($P > 0.05$) (Fig. 3A and D).

Sobotnik et al. (2008) reported that termites often perform antennal inspection (antennation) when they first come into contact with another termite and this scenario corresponds well with the results of this study. Upon encountering another termite, examination of the opponent species was more frequent than any other behavior. *C. gestroi* was more active in seeking such interactions with *M. crassus* than the other way around.

After antennation, other behaviors were exhibited by *M. crassus*, namely, jerking, avoidance, chasing/escaping, attack, defecation, grappling, and biting. Most of these behaviors were exhibited at a similar rate of frequency (Fig. 3).

M. crassus and the three opponent species avoided one another by rapidly moving away to prevent contact. *M. crassus* workers avoided the worker castes of *C. gestroi* significantly more (Fig. 3A) than they avoided the worker castes of *G. sulphureus* and *Odontotermes* sp. ($P < 0.05$). In contrast, soldiers of *M. crassus* hardly ever avoided either caste of the opponent species when they encountered them (Fig. 3C and D). A similar result was recorded between *M. crassus* workers and soldiers of the opponent species.

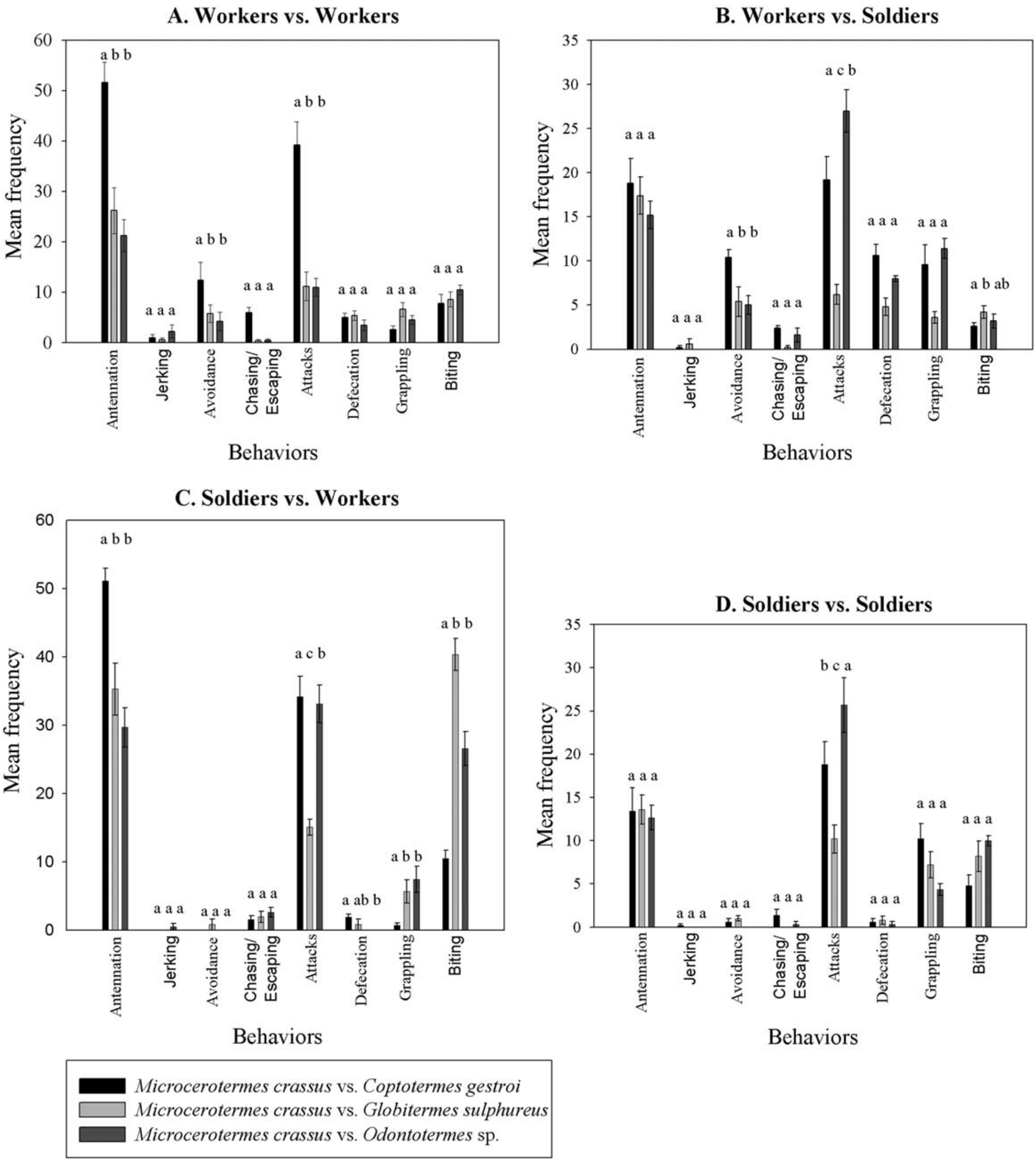

Fig. 3. Mean frequency of different behaviors (mean % ± SEM) exhibited by *M. crassus* of various caste combinations toward other termite species over a period of 5 min ($P < 0.05$; Kruskal–Wallis).

Sometimes, instead of avoiding the opponent species, they chased each other.

M. crassus attacked its opponent by lunging forward. Attacks were directed toward the abdomen and thorax of the opponent species. Both castes of *M. crassus* attacked *C. gestroi* workers significantly more (Fig. 3A and C) than workers of *G. sulphureus* ($P < 0.05$). However, both castes of *M. crassus* attacked soldiers of *Odontotermes* sp. more frequently (Fig. 3B and D) than soldiers of the other two species ($P < 0.05$).

When entangled with an opponent, *M. crassus* may defecate on it by bending the tip of the abdomen upwards and depositing a droplet of anal fluid. All interaction shows that the frequency of *M. crassus* defecating on other termite species were relatively similar. We also observed termites locked together using their mandibles, and in such situations both termites held on and tried to drag each other along. This grappling position could last up to several minutes until both individuals let go or another individual came into contact with them and attacked either one of them.

In the worker–soldier interactions (Fig. 3B), the biting behavior exhibited by *M. crassus* differed significantly between *C. gestroi* and *G. sulphureus* ($P < 0.05$). Grappling and biting was less frequently ($P < 0.05$) exhibited by *M. crassus* soldiers toward workers of *C. gestroi* compared with that exhibited toward the worker caste of *G. sulphureus* and *Odontotermes* sp. (Fig. 3C). Binder (1988) described biting as a fatal snap, which results in the mandibles penetrating the head, thorax, or abdomen of the opponent. In our study, the bites of *M. crassus* sometimes excised the appendages of opponent species; in some cases even the head capsule of the opponent species was removed. Our study also showed that *M. crassus* soldiers made several additional contacts after a fatal snap was delivered; in some cases more snaps were made before the soldier moved away from the opponent species. At times, soldiers would further examine the defeated termite without biting it again.

When the behaviors of the opponent species were examined, soldiers of *C. gestroi* were aggressive toward both castes of *M. crassus. G. sulphureus* workers were aggressive when they encountered soldiers of *M. crassus. Odontotermes* sp. was less aggressive toward all caste combinations of *M. crassus* compared with *C. gestroi* and *G. sulphureus.*

Aggressive behavior does not necessarily guarantee survival or a higher chance of winning an encounter. Table 2 shows the survival of both *M. crassus* and the opponent species 24 h after the initial encounter. Workers of *M. crassus* were not competitive toward the worker caste of *C. gestroi* and *G. sulphureus* with 0% survival. However, *C. gestroi* was competitive toward *M. crassus,* whereas *G. sulphureus* was less competitive toward *M. crassus.*

In the worker–soldier interactions, survival between all species pairings differed significantly ($P < 0.05$). *Nasutitermes corniger* (Motschulsky) workers can act as very useful and capable defensive units, and a number of termite species are reported to exhibit violent agonistic responses, such as dismemberment of intruders by workers or in some cases by soldiers (Thorne 1982). Although *M. crassus* workers attacked or reacted aggressively toward the soldiers of the other three opponent species, in the end they succumbed to the injuries inflicted by the soldiers of all three species. Binder (1988) reported that workers of *H. aureus* were aggressive in the absence of soldiers; in the situation in which *H. aureus* had to deal with soldiers, although many workers were killed by the soldiers, this termite species still managed to subdue the attacks. Thus, if the number of *M. crassus* workers had been much higher compared with the number of opponent soldiers, perhaps more *M. crassus* workers could have survived the soldier attacks.

In soldier-worker encounters, *M. crassus* soldiers had a relatively low survival rate. In the opponent species, survival was low for workers of *C. gestroi,* and none of the workers of *G. sulphureus* and *Odontotermes* sp. survived the battle. All soldier-worker pairings showed a distinct difference in survival ($P < 0.05$), with the exception of the survival of *M. crassus* soldiers versus *C. gestroi* workers ($P > 0.05$) (Table 2). Both the termite species fought and suffered the same losses.

Table 2. Termite survival (%) (mean ± SEM) for different pairings after 24 h

Combination[a]	Survival (mean % ± SEM)[b,c]	
	MC	Opponent species (e.g. CG, GS and Od)
MC worker vs. CG worker	0.0 ± 0.0a (NC)	56.0 ± 2.5b (C)
MC worker vs. GS worker	0.0 ± 0.0a (NC)	6.0 ± 4.0b (LC)
MC worker vs. Od worker	0.4 ± 0.2a (LC)	0.0 ± 0.0a (NC)
MC worker vs. CG soldier	0.0 ± 0.0a (NC)	100.0 ± 0.0b (VC)
MC worker vs. GS soldier	0.0 ± 0.0a (NC)	50.0 ± 7.1b (C)
MC worker vs. Od soldier	0.0 ± 0.0a (NC)	8.6 ± 0.5b (LC)
MC soldier vs. CG worker	4.0 ± 4.0a (LC)	6.0 ± 4.0a (LC)
MC soldier vs. GS worker	14.0 ± 4.0a (LC)	0.0 ± 0.0b (NC)
MC soldier vs. Od worker	6.0 ± 1.1a (LC)	0.0 ± 0.0b (NC)
MC soldier vs. CG soldier	0.0 ± 0.0a (NC)	46.0 ± 8.1b (MC)
MC soldier vs. GS soldier	6.0 ± 4.0a (LC)	6.0 ± 6.0b (LC)
MC soldier vs. Od soldier	1.7 ± 0.3a (LC)	0.0 ± 0.0a (NC)

[a] MC, *M. crassus;* CG, *C. gestroi;* GS, *G. sulphureus;* Od, *Odontotermes* sp.

[b] Means followed by the same letter within the same row of each combination are not significantly different at $\alpha = 0.05$ (paired *t*-test).

[c] Mean survival of 0%, not competitive (NC); >0–< 25%, less competitive (LC); 25%, <50%, moderately competitive (MC); 50–<75%, competitive (C); 75–<100%, very competitive (VS).

Survival in soldier-soldier encounters differed significantly only for *M. crassus* and *C. gestroi* encounters ($P < 0.05$). The soldiers of *M. crassus* were very competitive to being killed by *C. gestroi* soldiers, whereas *C. gestroi* soldiers were only moderately competitive to being killed by *M. crassus* soldiers. In confrontations with soldiers of *G. sulphureus* and *Odontotermes* sp., *M. crassus* also had low survival ($P > 0.05$). Overall, these results show that although *M. crassus* can be aggressive when encountering termites of other species, they are poor fighters with low survival rates.

Our study provides a deeper insight into intra- and interspecific interactions between *M. crassus* and pest species inhabiting the community around buildings (and no doubt in other habitats where these species co-occur). The intensity of agonistic responses and the frequency of particular behaviors differed according to the opponent species. No aggression was detected between different colonies of *M. crassus* from widely separated areas. In contrast, *M. crassus* showed a variety of agonistic behavior in interspecific encounters against *C. gestroi, G. sulphureus,* and *Odontotermes* sp.

Acknowledgments

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