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BEHAVIOR OF *RETICULITERMES FLAVIPES* (ISOPTERA: RHINOTERMITIDAE) DURING COLONY FUSION

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Abstract Limited data exist on foraging, agonistic and feeding behavior of subterranean termites of the same species but from different colonies. We conducted research to determine if subterranean termites, *Reticulitermes flavipes* (Kollar) from different colonies may express unusual foraging, agonistic and feeding behavior during colony fusion at various temperatures. Fifty *R. flavipes* workers from two different colonies (colony #1 undyed and colony #2 dyed with Nile blue-A)) were placed in separate feeding chambers and connected with polyethylene tubes to a common feeding chamber for foraging interaction at 15, 20, 23, 25 and 30°C. Each treatment had three replications. Data were recorded on foraging, agonistic/aggressive behavior and food consumption of termite workers at 1, 3, 24, 72 h and 7, 14 and 21 d intervals. Our data revealed that different colony members did not display agonistic behavior and fused together at 15-25°C with maximum food consumption at 20°C. Food consumption was not significantly different ($P \geq 0.05$) at 15-30°C and the 30°C was not the optimum temperature for termite survival.
Key words Subterranean termites, *R. flavipes,* agonistic behavior.

INTRODUCTION

Agonistic behavior refers to the social interaction of aggressive responses when new termite workers from the same species but different colonies are introduced (Haverty and Thorne, 1989). There are very few reports on Reticulitermes spp. of such interactions in North America, with the exception of Zootermopsis spp. (Haverty and Thorne, 1989; Thorne and Haverty, 1991), Heterotermes spp. (Binder, 1988; Jones, 1993), Coptotermes formosanus Shiraki (Su and Scheffrahn, 1988; Shelton, 1997a, b). The fundamental mechanisms associated with agonistic responses in subterranean termites are highly variable. When reproduction within the colony is controlled by a single king and queen, the colony is referred to as a simple family. After the death of one or both primary reproductives, the colony may undergo several cycles of inbreeding by the secondary neotenics. This is referred to as an extended family. Termite colonies have been also known to fuse together (DeHeer and Vargo, 2004, 2008; Johns et al., 2009). In certain cases, when workers within a colony express genetic ancestry to more than one colony, it is known as fused or mixed family. Colony fusion is difficult to detect when colonies have a complex genetic architecture, for example, when queen has multiple mating or when multiple queens reproduce offsprings (DeHeer and Vargo, 2004, 2008).

Haverty and Thorne (1989) reported that the termite colony members will act aggressively towards individuals from other nest-mates during nest-mate recognition phase. However, the level of inter-colony aggression within a species varies from one colony to another one. Studies on *C. formosanus* have demonstrated that inter-colony agonistic behavior does not always result from pairing colonies in the laboratory (Su and Haverty, 1991). Clement (1986) reported that colonies of

Reticulitermes spp. either accept or reject other colony members but it depends on the seasonal change (spring, summer or fall) during the termite collection. However, Grace (1996) did not see any agonistic behavior in *R. flavipes* colonies collected in the fall, whereas Clement (1986) suggested that European *Reticulitermes* colonies were rejecting other colony members.

Reticulitermes termite nestings were grouped into multiple-site nesters (Shellman-Reeve, 1997). When the wood as food source is depleted, the colony migrates to another suitable wood resource. *Reticulitermes* termite wood preference depends on wood species, stage of decay and moisture content (Waller and LaFage, 1987). Moreover, preferred wood might have already been occupied by other inhabitants. If the migratory colony is not able to find new preferred wood resource, it is most likely to invade another colony to access new food resource. Consequently, the host colony will either fight or fuse with the invading colony (Shellman-Reeve, 1997).

In this study, we conducted experiments to determine foraging, agonistic, feeding behavior and colony fusion correlation while pairing workers from two distinct colonies of *R. flavipes* at five different temperatures.

MATERIAL AND METHODS

Source of Termites. Wood logs infested with subterranean termites were collected from two different locations ≈500 m apart and returned to the laboratory at the University of Nebraska-Lincoln. The termites were extracted from each log from two different colonies and were maintained in separate polyethylene hard-plastic containers with lids and covered with black plastic for creating the subterranean environment. Termites were allowed to acclimate by maintaining all containers at room temperature (23 ± 2°C) for 30 d.

Temperature Setting. Percival growth chambers (Percival Scientific Inc., Perry, IA) were preset at 15, 20, 23, 25 and 30°C. Twenty termite workers plus one soldier were placed in a plastic petri dish (100 x 15 mm) with moist sand and corrugated cardboard. Later, these petri dishes with termites were placed in growth chambers at preset temperatures to ascertain that termites could survive for 30 d.

Feeding Arenas. Feeding arenas were similar to those used by Binder (1988) and Grace (1996). Each arena consisted a set of three polyethylene petri dishes/feeding chambers (100 mm diameter x 15 mm height, BD Falcon company, Franklin Lakes, NJ) and connected with 2 cm long of 6.35 mm diameter polyethylene tubing to accommodate approximately 1,000 termites (Figure 1). Each arena consisted of ~5 g sterile sand. The pinewood pieces (1.0 cm length x 1.0 cm width x 2.5 cm height) were oven dried overnight (80°C), cooled and weighed before their use. Each pair of pinewood pieces weighed ~1.5 g. One of the termite colony groups was stained with 0.1% (wt/wt) Nile Blue A by a no choice feeding of stained filter paper (Whatman No. 1, 9.0 cm in diameter) for 5-7 d (Abdul Hafiz et al., 2007).

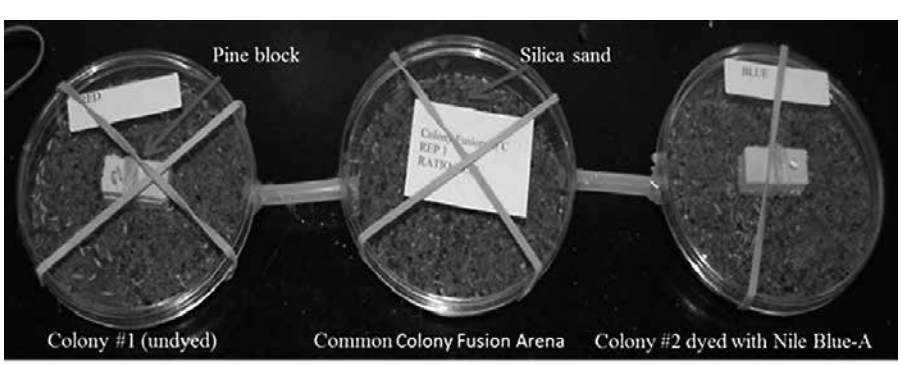

Figure 1. Feeding arena. Subterranean termites: Colony 1, undyed, Colony 2, dyed. Were placed in separate feeding chamber which were connected to a common arena and with food source in center

Feeding and Food Consumption. In the first experiment, 50 undyed termite workers from colony #1 were placed in the petri dish (feeding chamber) proximal of feeding arena and 50 Nile blue-A dyed termite workers from a colony #2 were placed in the petri dish (feeding chamber) distal to the feeding arena, leaving the middle petri dish (feeding chamber) unoccupied (Figure 1). Termite foraging activities were observed at intervals of 1, 3, 24, and 72 h and 7, 14 and 21 d. Food consumption was recorded at the end of 3 wk after dismantling the feeding arenas. The pair of pinewood pieces at each arena were cleaned, oven dried (80°C), cooled and weighted. The experiment design was the completely randomized block and each treatment had three replications. Analysis of variance (ANOVA) and *t*-tests (LSD) were conducted using SAS to test for significant differences in food consumption ($P \geq 0.05$).

Colony Merger/Fusion. In the second experiment, 50 undyed termite workers from colony #1 were placed in the petri dish (feeding chamber) proximal of feeding arena and 50 Nile blue-A dyed termite workers from a colony #2 were placed in the petri dish (feeding chamber) distal to the feeding arena, leaving the middle petri dish unoccupied (Fig. 1). The arenas were left on the laboratory bench for 30 min for acclimation. Each petri dish in the feeding arena was labeled reflecting appropriate treatment and the replication. The arenas were placed in 60.96 x 41.99 x 14.94 cm hard plastic boxes (Bella, Leominster, MA) covered with aluminum foil. Finally, the plastic boxes were placed in growth chambers that were programed for 15, 20, 23, 25 and 30°C. The sand in each petri dish was moistened weekly or as needed. Inter-colony pairings were monitored at intervals of 1, 3, 24, 72 h and 7, 14 and 21 d. After 3 wk of incubation, each feeding arena was dismantled and the number of undyed and blue dyed termites in each of the three petri dishes were recorded. For each test arena, connecting tubes were considered as part of the respective petri dish (feeding chamber). All colony pairing were categorized according to Fisher et al. (2004) as (a) sharing both nesting space food resources, (b) sharing food resources but maintaining separate nesting material or (c) maintaining separate nesting space not sharing food resources. Colony fusion was defined as the sharing of both nest sites and food resources.

Termite Mortality. After 3 wk of incubation, the feeding arenas were carefully dismantled. The number of blue dyed and undyed termites were recorded in each of three petri dishes (feeding chambers) for the pairing arenas (connecting tubes were considered part of the respective feeding chambers). Termite mortality was compared within each pairing for all five temperature settings using *t*-test (LSD). The data on termite mortality at respective temperature were subjected to analysis of variance (ANOVA) at the significance level of $P \leq 0.05$ using SAS (SAS Institute Inc. 2000).

Agonistic Behavior. The above described feeding arenas were used for observing agonistic/aggressive behavior at intervals of 1, 3, 24, 72 h, and 7, 14 and 21 d for all five temperature settings as mentioned earlier. Agonistic/aggressive behavior is defined as offensive and defensive responses between competing termite workers from two different colonies (King, 1973). The termites from pairing colonies were observed for 10 min at each time interval and at each temperature.

RESULTS

Feeding and Food Consumption

Termites fed actively at 15-25°C and the highest feeding was at 20°C with mean wood consumption of 0.34 g and the lowest feeding consumption at 15°C. The 25°C was considered the upper limit with mean

wood consumption of 0.29 g (Table 1). However, the *t*-test (LSD) indicated no significant differences in wood consumption amongst all temperatures (15, 20, 23, 25 and 30°C) ($P \geq 0.05$) (Table 1).

Colony Merger/Fusion

All fifteen termite colony-pairings (100%) shared both nesting areas and food resources at all temperatures until 21 d. In all colony pairings during the first hour at all temperature settings, the termites were still foraging within the original feeding chamber and searching for suitable nesting site and food source. At 25°C, all the pairings shared both nesting space and food resources. At 15, 20 and 23°C, only 33.3% of colony pairings shared both nesting space and food resources, while 66.7% termites shared food resources but maintaining separate nesting material. After 3 h, all the colony pairings were sharing both nesting spaces and food resources at 15-25°C. However, at 30°C only 33.3% of termites shared both nesting and food resources, while 66.7% termites shared food resources but maintained separate nesting materials (Table 2). After 24 h, all the colony pairings at all temperatures shared both nesting and food resources, and the termites were very active in all feeding chambers. After 14 d, all the pairings still shared both nesting space and food resources except at 30°C. In addition, at 30°C the termites were not actively moving in colony pairing. After 21 d, the termites in colony pairings shared both nesting areas and food resources at all temperatures. Furthermore, termites in colony pairings were sluggish at 30°C after 21 d. Termites in colonies that fused/merged were observed grooming, participating in trophallaxis and foraging with unrelated nest mates.

Termite Mortality

At 30°C, pairing-termites had 65-75% mortality (Table 3). The optimum temperature for the pairing-termites was 25°C with only 15-41% mortality. In addition, at 15, 20 and 23°C termites had <50% mortality. Based on *t*- test analysis, termite mortality did not differ significantly at 15 to 25°C except for 30°C ($P \leq 0.05$) (Table 3). Temperature setting from 15 to 25°C also can be ideal temperatures for the termite pairings and colony fusion. Overall, temperatures have a significant effect on termite mortality ($P \leq 0.05$).

Agonistic/Aggressive Behavior

Our data indicated that termites show agonistic behavior for the first 3 h. This behavior was observed with head banging against each other. However, no agonistic/aggressive behavior was observed in termite colony-pairings after 24 h until 21 d.

Table 1. Mean food consumption by *Reticulitermes flavipes* after 21 days. Means with the same letter are not significantly different, $P \leq 0.05$.

Temperature (°C)	No. replicates	Mean* food consumed (g) ± SD
15	3	0.29 ± 0.04 [a]
20	3	0.34 ± 0.02 [a]
23	3	0.30 ± 0.04 [a]
25	3	0.29 ± 0.03 [a]
30	3	0.33 ± 0.03 [a]

Table 2. Colony fusion of *Reticulitermes flavipes* observed after 1, 3, 24, 72 hours, and 7, 14 and 21 days. A: Sharing both nesting space food resources; B: Sharing food resources but maintaining separate nesting material; C: Maintaining separate nesting space not sharing food resources

Temp.	Reps.	Time Interval							
		1h	3h	24h	48h	72h	7d	14d	21d
15^{0}C	Rep 1	A	A	A	A	A	A	A	A
15^{0}C	Rep 2	B	A	A	A	A	A	A	A
15^{0}C	Rep 3	B	A	A	A	A	A	A	A
20^{0}C	Rep 1	B	A	A	A	A	A	A	A
20^{0}C	Rep 2	A	A	A	A	A	A	A	A
20^{0}C	Rep 3	B	A	A	A	A	A	A	A
23^{0}C	Rep 1	A	A	A	A	A	A	A	A
23^{0}C	Rep 2	B	A	A	A	A	A	A	A
23^{0}C	Rep 3	B	A	A	A	A	A	A	A
25^{0}C	Rep 1	A	A	A	A	A	A	A	A
25^{0}C	Rep 2	A	A	A	A	A	A	A	A
25^{0}C	Rep 3	A	A	A	A	A	A	A	A
30^{0}C	Rep 1	C	A	B	A	A	A	A	A
30^{0}C	Rep 2	B	B	A	A	A	A	A	A
30^{0}C	Rep 3	B	B	A	A	A	A	A	A

Table 3. Mean individual *Reticulitermes flavipes* mortality of (colony #1 plus colony #2) for each pairing colonies after 21 days. Means followed by same letter not significantly different $P \leq 0.05$.

Temperature (^{o} C)	Replicates	Total percent termite mortality in individual feeding chamber (Col.1 + Col. 2) $\pm$ SD	Total percent mortality after pairing, Colony 1 + Colony 2
15	3	22.83 $\pm$ 8.30 b	<50%
20	3	18.67 $\pm$ 10.51 b	<50%
23	3	22.00 $\pm$ 8.34 b	<50%
25	3	18.67 $\pm$ 6.73 b	15% - 41%
30	3	33.67 $\pm$ 13.66 a	65% - 75%

DISCUSSION

Our data suggest that optimum temperature range and suitable food resources are inter-related for foraging and colony fusion. According to our data, the field collected subterranean termite colonies from different locations can merge/fuse together in the laboratory conditions at 15-25^{o}C. However, the temperature >30^{o}C may delay the termite colony-fusion process. According to Grace (1996) less agonistic behavior in introduced populations of termites in Toronto, Canada can lead to colony merging. A laboratory study conducted by Fisher et al. (2004) indicated that fused colonies can develop new functional replacement reproductives originating from only one colony. Fisher et al. (2004) further reported that there was no evidence of interbreeding by the secondary reproductives originating from

two different colonies. Matsuura and Nishida (2001) suggested merging increases the colony size and it may have adaptive significance under certain environment conditions. In addition, Matsuura and Nishida (2001) found that colony fusion might be related to the nymph ratio in a colony. These authors denoted that the host colony showed agonistic behavior if the intruder colony had a higher nymph ratio than the host colony. But, if the host colony had a higher nymph ratio the intruder colony will merge.

In our study, agonistic behavior was only observed during first 3 h for termite colony-pairing at all temperature settings. Several studies on ants and termites indicated low genetic differences in nearby termite colonies which may be associated with low aggression (Beye et al., 1997; Husseneder et al., 1998; Tsutsui et al., 2000). Colony fusion due to recognition errors is one mechanism that can allow the formation of complex termite colonies reminiscent of ant super colonies (DeHeer et al., 2005). Most *Nasutitermes corniger* (Motschulsky) colonies are simple families, with a single queen and king (Atkinson and Adams, 1997); however, natural populations also include colonies with multiple unrelated queens and up to 50 nests. According to Pedersen et al. (2006) *N. corniger* from different nests within the same complex colony are mutually tolerant, but are highly aggressive toward other colony members of the same species. In addition, genetic bottlenecks have been hypothesized to explain loss of aggression among social groups, allowing the formation of complex colonies (Tsutsui et al., 2000). When colony recognition cues are heritable, loss of genetic diversity can result in greater similarity among colonies, reducing the ability of insects to discriminate against non-nestmates.

In addition, individual agonistic behavior varies. In a study using workers of *R. flavipes* and *R. virginicus,* only 4.5% of arenas with intraspecific colony pairs displayed agonistic behavior (Polizzi and Forschler, 1999). When agonistic behavior of individual workers of *R. flavipes* and *R. virginicus* was examined, 89% of previously aggressive workers displayed aggression during a second test, while 88% of previously passive workers were passive during a second test (Polizzi and Forschler, 1999). Therefore, there could be a division of labor among termite workers regarding the display of aggressive behavior (Polizzi and Forschler, 1999). Furthermore, it has been suggested that the mechanism of kin recognition involves multiple stimuli, including chemical, a behavioral and digestive cues (Thorne and Haverty,1991). Cuticular hydrocarbon composition differences on the epicuticle of *C. formosanus* were not correlated with inter-colony agonistic behavior (Su and Haverty, 1991). Agonistic behavior of *C. formosanus* colonies from Hawaii and Florida was not correlated with geographic distance (Su and Haverty, 1991; Shelton and Grace, 1997a). In addition, aggressive behavior between *C. formosanus* colonies in Hawaii did not correlate with genetic similarities between colonies (Husseneder and Grace, 2001). In our study, no agonistic behavior was observed at lower or higher temperatures after 24 h. Low temperature conditioning reduced inter-colony agonistic behavior presumably due to the elimination or suppression of kin recognition cues (Shelton and Grace, 1997b). Colony pairs of laboratory-reared *C. formosanus* did not display any agonistic behavior although these same colony pairs did display agonistic interactions when field collected termites were used (Shelton and Grace, 1997a).

In our study, temperatures around 15-25^{o}C are considered to be optimal for the termites to be actively interacting with each other. Again, no clear agonistic display was observed, but at 30^{o}C the termite activity seemed to be slower after two weeks of pairing. The field collected *Reticulitermes spp.* studied by Getty et al. (2000) showed an agonistic behavior in laboratory conditions for over 18 m. Fisher et al. (2004) witnessed that intruding termites performed maintenance behavior like grooming and trophallaxis. Similar observations were recorded in our study where most of the workers were grooming each other including the intruder workers at 15-25^{o}C. At 30^{o}C the termites seems to groom actively for first 72 h but grooming declines after one wk.

CONCLUSIONS

Colony merger/fusion can occur in the laboratory at 15, 20, 23, 25 and 30°C. Termite feeding activities were prolific at 15-25°C. All termites in colony pairings forage actively the first 72 h but least activity was observed at 30°C after 2 wk. Termite mortality was proportionately increased at 30°C after 3 wk.

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