

Effect of Two Ant Species (Hymenoptera: Formicidae) on the Foraging and Survival of the Formosan Subterranean Termite (Isoptera: Rhinotermitidae)

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ABSTRACT We examined the effect of 2 ant species, the bigheaded ant, *Pheidole megacephala* (F.), and *Ochetellus glaber* (Mayr), on the Formosan subterranean termite, *Coptotermes formosanus* Shiraki. We also examined how differences in the proportion of termite soldiers affected the susceptibility of *C. formosanus* to predation by *P. megacephala*. In sand-filled containers, *C. formosanus* was more vulnerable to predation by *P. megacephala* than by *O. glaber*. However, the presence of ants of either species caused substantial mortality of termite soldiers. *P. megacephala* was much more invasive of termite galleries than *O. glaber*. Termites exposed to *P. megacephala* suffered greater mortality compared with controls, regardless of worker to soldier ratio. However, there was no difference in termite mortality among replicates with different worker to soldier ratios. In the absence of sand, both ant species caused 100% mortality of termites after 1 wk of exposure.

KEY WORDS ants, *Coptotermes formosanus*, predation

SUBTERRANEAN TERMITES ARE major pests of wood products. Efforts to control the Formosan subterranean termite, *Coptotermes formosanus* Shiraki, in the Hawaiian islands cost at least \$60 million each year (Yates and Tamashiro 1990). A mature *C. formosanus* colony contains 2-4 million termites on average (Su and Scheffrahn 1988). The main and satellite nests of *C. formosanus* can occur anywhere within a foraging area of >200 m in diameter (Su and Tamashiro 1987). *C. formosanus* is also capable of establishing aerial colonies with no connection to the ground. Because of these characteristics, *C. formosanus* is very difficult to control.

Prevention of termite infestations of buildings in Hawaii has relied primarily on the use of insecticide applications to the soil (Tamashiro et al. 1990, Grace et al. 1993a). However, the longevity of most soil insecticides is quite limited under tropical conditions (Grace et al. 1993b). Hence, there is a need to develop more permanent methods of controlling termite infestations. As with other insect pests, biological control agents could be an important component of an integrated approach to the management of termite populations.

Ants are considered to be important biological control agents against insect pests in agricultural and agroforestry systems (Jones and Sterling 1979, Majer 1982, Carroll and Risch 1990, Perfecto 1991). Ants are also major enemies of termites (Deligne et al. 1981, Hölldobler and Wilson 1990). Ants may play an important role in limiting termite

distribution through predation, competition for nesting sites, and disruption of foraging activities. In this study, we examined the effect of 2 ant species on *C. formosanus* in sand-filled containers where termites were able to construct galleries in the sand that served as barriers against ant attacks.

We also examined how differences in the proportion of termite soldiers affected the susceptibility of *C. formosanus* to ant predation. Other research has shown that *C. formosanus* is more vulnerable to predation by the red imported fire ant, *Solenopsis invicta* Buren, when the proportion of soldiers is low (Wells and Henderson 1993). In that study, however, termites were not able to construct physical barriers and had to rely primarily on soldiers to ward off ant invasion. In our study, we examined the effect of ants on groups of termites with different proportions of soldiers in a situation where they were also able to use physical barriers as a defense.

Materials and Methods

Formosan subterranean termites were collected from a field colony on the Manoa campus of the University of Hawaii using a trapping technique described by Tamashiro et al. (1973) in which foraging termites were collected in boxes constructed of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, lumber. A wooden stake was placed in the ground and covered by a wooden box. The box was protected by a 22.5-liter cylindrical metal can with the bottom removed, which was placed over each

Table 1. Percentage of mortality of Formosan subterranean termites (worker to soldier ratio of 360:40) in sand-filled containers introduced into fluon-coated boxes containing ant colonies

Ant species	Mean % termite mortality \pm SD					
	10-d Exposure			30-d Exposure		
	Replicates	Workers	Soldiers	Replicates	Workers	Soldiers
Control	19	10.9 \pm 4.9a	8.2 \pm 5.8a	10	10.9 \pm 5.0a	8.0 \pm 7.9a
<i>O. glaber</i>	5	13.2 \pm 3.2a	38.0 \pm 28.8b	10	11.4 \pm 7.0a	29.5 \pm 27.0b
<i>P. megacephala</i>	10	32.6 \pm 37.4b	57.5 \pm 32.0b	17	47.6 \pm 44.7b	63.4 \pm 39.2b

Means in the same column followed by the same letter are not significantly different ($P = 0.05$; Tukey studentized range test [SAS Institute 1987]). ANOVA for 10-d exposure: workers, $F = 3.55$, $df = 2$, $P = 0.04$; soldiers, $F = 18.71$, $df = 2$, $P = 0.0001$. For 30-d exposure: workers, $F = 5.66$, $df = 2$, $P = 0.0075$; soldiers, $F = 10.5$, $df = 2$, $P = 0.0003$.

box and covered with a metal sheet. Termites were collected immediately before their use in laboratory assays.

Termites were placed in plastic screwtop jars (8 cm diameter by 10 cm high), each containing 300 g of silica sand and 60 ml of distilled water to provide moisture, and maintained in the laboratory at ambient conditions (23–25°C). Container lids were left on loosely so that containers were not airtight. Food was provided by placing 2 pieces of wooden tongue depressor (Hardwood, Guilford, ME), 4 cm in length, at the bottom of each container. Termites were allowed to acclimate and build galleries in the sand for 1 wk before experiments began.

The 2 ant species used in this study, the big-headed ant, *Pheidole megacephala* (F.), and *Ochetellus glaber* (Mayr), frequently invade our termite collection traps and nest in termite galleries (unpublished data). Both ant species will readily prey on termites when placed in boxes containing ant colonies in an exposed situation. Ant colonies were collected on campus and maintained in the laboratory at ambient conditions (23–25°C) in uncovered plastic boxes (30 by 16 cm). The sides of the boxes were coated with liquid teflon (Fluon, Northern, Woonsocket, RI) to prevent ants from escaping. Each box contained a plastic petri dish (4.5 cm diameter) with a layer of plaster of paris in the bottom and a red cellophane-covered lid to provide a suitable nesting site for ants. Ants were able to freely enter and leave the dish through a hole in the lid. They were provided with a constant supply of water from a water-filled 15-dram plastic vial with small holes in the sides and positioned upside down in the ant box so that ants could collect water droplets when needed. Each box also contained a cap of a plastic Falcon test tube (17 by 100-mm) filled with honey. Freshly killed (by heating in a microwave) Formosan subterranean termites were added to boxes for protein approximately once a week.

Three experiments were conducted in which the number of termites in each container was 400 and the ant colonies consisted of 1,000 workers, 1 queen, and 20–30 larvae of various instars. For *P. megacephala*, there were 950 minor and 50 major workers. Termite nesting containers were placed in the Fluon-coated boxes containing ant colonies.

Ants gained access to the termites through the loosely fitting container lids. In the 1st experiment, termites in each container consisted of a 360 worker to 40 soldier ratio, which approximates the natural caste distribution observed in the field (Haverty 1977), and termite containers were introduced into boxes containing either *P. megacephala* or *O. glaber* for 10 d. In the 2nd experiment, termite groups with a worker to soldier ratio of 360:40 were introduced into boxes containing either *P. megacephala* or *O. glaber* for 30 d. Also, termite groups with worker to soldier ratios of 380:20 and 400:0 were introduced into boxes containing *P. megacephala* for 30 d. In the 3rd experiment, termite groups with a worker to soldier ratio of 360:40 were placed in containers without sand and introduced into boxes containing either *P. megacephala* or *O. glaber* for 7 d. Termites were provided with 3 filter paper disks (5.5 cm diameter) moistened with distilled water every other day to provide moisture and food. For all 3 experiments, containers of termites of each worker to soldier caste ratio were kept in an ant-free environment to serve as controls. Containers were checked every other day and observations of ant-termite encounters and ant invasions of termite galleries were recorded.

At the conclusion of each experiment, proportional termite mortality was transformed by the arcsine of the square root (Sokal and Rohlf 1981) and subjected to analysis of variance (ANOVA) using the general linear models procedure and means were separated by the Tukey studentized range test ($P < 0.05$) (SAS Institute 1987).

Results

Results from termite exposures to ants that lasted 10 and 30 d were similar (Table 1). Mortality of both termite workers and soldiers was greater in containers exposed to *P. megacephala* than in controls. Termite soldier mortality was greater in replicates exposed to *O. glaber* than in controls, but there was no difference in termite worker mortality between replicates exposed to *O. glaber* and controls (Table 1). In nesting containers without sand, termites suffered 100% mortality after 1 wk of exposure to ants of either species (Table 2). Termites exposed to *P. megacephala* for 30 d suffered

Table 2. Percentage of mortality of Formosan subterranean termites (worker to soldier ratio of 360:40) in containers without sand introduced into fluron-coated boxes containing ant colonies for 7 d

Ant species	Mean % termite mortality \pm SD		
	Replicates	Workers	Soldiers
Control	5	9.3 \pm 5.15a	6.0 \pm 4.18a
<i>O. glaber</i>	5	100.0 \pm 0.0b	100.0 \pm 0.0b
<i>P. megacephala</i>	5	100.0 \pm 0.0b	100.0 \pm 0.0b

Means in the same column followed by the same letter are not significantly different ($P = 0.05$; Tukey studentized range test [SAS Institute 1987]).

greater mortality compared to controls, regardless of worker to soldier ratio, and there was no difference in termite mortality among replicates with different worker to soldier ratios (Table 3). In containers where ants had completely broken through termite galleries and invaded the entire container, there was 100% termite mortality. In contrast, mortality of termite workers in containers where there was at least 1 termite gallery that had not been invaded by ants was similar to mortality in controls, even if almost the entire container had been invaded by ants and termites were restricted to only a small area on the bottom of the container.

Pheidole megacephala was much more aggressive at moving into the sand and more invasive of termite galleries than *O. glaber*. *P. megacephala* had completely invaded the entire container, broken through all termite galleries and caused 100% termite mortality in 20% of replicates after 10 d. After 30 d, *P. megacephala* had completely invaded 55% of replicates with a 400:0 worker soldier ratio compared with only 35 and 30% of replicates with 360:40 and 380:20 ratios, respectively. Also, *P. megacephala* moved its nest into the termite nesting containers in 70% of replicates in the 10 d experiment. In the 30-d experiment, *P. megacephala* moved its nest into termite containers in 65, 50, and 78% of replicates with a 360:40, 380:20, and 400:0 worker to soldier ratio, respectively. As *P. megacephala* moved deeper into the sand, termites became restricted to a small area on the bottom of the container and were precluded from foraging outside of that area. We observed large numbers of *P. megacephala* attacking and dragging away both termite workers and soldiers.

In contrast, *O. glaber* did not move its nest into containers or invade termite galleries in any of the replicates. In several replicates, *O. glaber* penetrated into the top layer of sand 1–4 cm. However, we only observed encounters between foraging *O. glaber* and termite soldiers guarding tunnel entrances. We did not observe *O. glaber* entering termite galleries.

Discussion

Coptotermes formosanus was more vulnerable to predation by *P. megacephala* than by *O. glaber* in

Table 3. Percentage of mortality of Formosan subterranean termites with different worker to soldier caste ratios in sand-filled containers introduced into fluron-coated boxes containing *P. megacephala* colonies for 30 d

Worker to soldier ratio	Ants	Replicates	Mean % termite mortality \pm SD
360:40	Present	17	49.2 \pm 43.6a
	Absent	10	10.65 \pm 4.5b
380:20	Present	10	60.8 \pm 38.5a
	Absent	10	6.5 \pm 2.5b
400:0	Present	9	72.8 \pm 38.3a
	Absent	10	17.5 \pm 7.9b

Means in the same column followed by the same letter are not significantly different ($P = 0.05$; Tukey studentized range test [SAS Institute 1987]). ANOVA: $F = 8.06$, $df = 5$, $P = 0.0001$.

sand-filled containers. However, in the absence of sand, there was 100% mortality of termites exposed to either ant species after only 1 wk. Although exposure to *O. glaber* did not affect the survival of termite workers in sand-filled containers, the presence of ants of either species caused substantial mortality of termite soldiers. Termite soldiers are specialized for defense and they actively defend entrances to termite galleries (Deligne et al. 1981). Termite soldiers were killed during encounters with foraging *O. glaber*, even though *O. glaber* did not invade termite galleries in the sand.

Pheidole megacephala may also have an effect on subterranean termites by disrupting their foraging activities and limiting their access to food sources and nesting sites. In the majority of containers, these ants severely restricted termite foraging by taking over their galleries. *O. glaber* was less invasive than *P. megacephala* and did not seem to have any negative effect on termite foraging in sand-filled containers.

Our field observations (unpublished data) indicate that *P. megacephala* is particularly aggressive in occupying termite galleries in our termite traps located on the campus of the University of Hawaii at Manoa and elsewhere on the island of Oahu. In previous research, we also observed that a greater proportion of *C. formosanus* soldiers responded aggressively to *P. megacephala* than to 6 other ant species. In experiments using freshly killed ants, 63% of *C. formosanus* soldiers responded aggressively to *P. megacephala*, whereas only 6% responded aggressively to *O. glaber* (Cornelius and Grace 1994b). In experiments where groups of termites and ants were placed together in arenas and termite soldiers engaged in combat with ants, termites caused greater mortality of *P. megacephala* than *O. glaber* or *Tetramorium simillimum* (F. Smith), apparently because the aggressive behavior of *P. megacephala* toward termites increased its likelihood of becoming engaged in combat with termite soldiers (Cornelius and Grace 1995).

In contrast, *C. formosanus* often avoids contact with freshly killed *O. glaber*. *O. glaber* is a member

of the subfamily Dolichoderinae, which uses anal gland secretions to repel other ant species (Cavill et al. 1982, Scheffrahn et al. 1984). *C. formosanus* avoids contact with filter paper disks treated with extracts of *O. glaber* and will not penetrate *O. glaber* extract-treated sand barriers for at least 10 d (Cornelius and Grace 1994a). Furthermore, extract-treated sand is toxic to termites when they are continuously exposed to it for 24 h (Cornelius et al. 1995). Although *O. glaber* secretes chemicals that are potentially toxic to *C. formosanus* and will prey on termites when they are placed in ant boxes in an exposed situation, *C. formosanus* was able to avoid predation by *O. glaber* by constructing galleries in the sand.

The most effective method of defense used by termites to avoid ant predation is to construct physical barriers of soil, masticated wood, and salivary secretions (Deligne et al. 1981). Termite workers were able to avoid predation by *O. glaber* by constructing galleries in the sand that acted as physical barriers. Also, there was relatively low mortality of termite workers in containers invaded by *P. megacephala* unless ants had successfully invaded all of the termite galleries in a container. Therefore, some termite workers were able to escape predation by *P. megacephala* even in the absence of soldiers in sand-filled containers for a month.

Because food (wood) was located on the bottom of the container, termite workers were able to survive in containers invaded by *P. megacephala* so long as they maintained a refuge. Hence, there were no differences in termite mortality among containers with different worker to soldier ratios. However, mortality was >70% in replicates with no soldiers compared with <50% in replicates with 10% soldiers and there were 20% more replicates which were completely taken over by ants in the absence of soldiers compared with replicates with 10% soldiers, suggesting that soldiers are important for termite defense against ants. Other research has shown that having a greater proportion of soldiers present increases the survivorship of *C. formosanus* subjected to ant predation when physical barriers are absent (Wells and Henderson 1993).

Termite soldiers also play an important role in protecting foragers against ants. Having a greater proportion of soldiers in foraging groups could enable termites to expand their foraging areas. In laboratory tests, *C. formosanus* was less likely to move into new areas when a small number of soldiers was present (Wells and Henderson 1993). Although *C. formosanus* workers in this study were able to survive invasion by *P. megacephala* in the absence of soldiers, they were not able to build galleries to forage for food. Further research is necessary to assess the importance of termite soldiers in contributing to the movement of *C. formosanus* foragers into new areas.

Although ants are considered to be pests when they forage and nest inside of buildings, they are important natural enemies of subterranean termites in the surrounding urban environment. Our results indicate that *P. megacephala* has the potential to play a role in limiting subterranean termite populations nesting in the ground through predation and disruption of foraging activities and could possibly be a component of an integrated pest management program by reducing termite numbers and restricting the ability of termites to move into new areas near threatened structures.

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