

Laboratory Evaluations of Interactions of Three Ant Species with the Formosan Subterranean Termite (Isoptera: Rhinotermitidae)

by

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ABSTRACT

We compared the interaction of *Coptotermes formosanus* Shiraki with three generalist ant predators, *Pheidole megacephala* (Fabricius), *Ochetellus glaber* (Mayr), and *Tetramorium simillimum* (F. Smith) in a laboratory arena and determined if there were differences in the susceptibility of *C. formosanus* to attack by these ant species and of the ants to termite defenses. *T. simillimum* caused significantly greater mortality of termite soldiers in the first experiment and of termite workers in the second experiment. *T. simillimum* appeared to be more effective at attacking termites in this study because termites did not immediately retreat upon contact with these ants and therefore were more likely to encounter *T. simillimum*. Mortality of *P. megacephala* was significantly greater than mortality of the other two ant species. *P. megacephala* appeared to be more aggressive toward termites and more likely to move into vials containing termites. Hence, *P. megacephala* may have suffered greater mortality because it was more likely to engage in combat with termite soldiers.

Key words: ant-termite interactions, *Coptotermes formosanus*, predation.

INTRODUCTION

Termites have evolved elaborate chemical and physical defenses to protect themselves against ants (Deligne *et al.*, 1981; Hölldobler & Wilson, 1990). For example, defensive secretions of termite soldiers of many species are repellent and/or toxic to ants (Mill, 1983; Scheffrahn *et al.*, 1987). Also, *Skatitermes watti* Coaton workers release a defensive secretion in response to ants or foreign termites that evokes an aggressive reaction from other workers in the same colony (Kistner 1975). Ant predation may have also influenced the evolution of termite foraging systems. For instance, the soldier, rather than the worker, caste of the termite, *Nasutitermes costalis* (Holmgren), initiates exploration into new areas in search of food. It is very unusual for the soldier

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caste in social insects to function as scouts and it appears that *N. costalis* evolved this foraging strategy to avoid ant predation (Traniello, 1981).

Several studies have examined interactions between termites and ants that are specialized termite predators (Longhurst *et al.*, 1978b; Longhurst *et al.*, 1979a; Maschwitz and Schönege, 1983). However, relatively few researchers have examined the defensive reactions of termites to attacks by generalist ant predators (Traniello, 1981; Wells & Henderson, 1993). This study compares the interaction of *Coptotermes formosanus* Shiraki with three generalist ant predators, *Pheidole megacephala* (Fabricius), *Ochetellus glaber* (Mayr), and *Tetramorium simillimum* (F. Smith).

Enemy specification, the triggering of specialized defensive behaviors upon contact with particularly threatening enemies, is common among ants (Hölldobler & Wilson, 1990). For instance, *Pheidole dentata* Mayr workers respond much more aggressively to ants in the genus *Solenopsis* than to other ant genera (Wilson, 1976). Some species of ants pose a much greater threat to termites than others. For example, certain ant species which are inquilines of termite mounds can actually provide benefits to termites by defending their mounds from attacks by other predaceous ants (Higashi & Ito, 1989). Hence, it is likely that termites would respond differently to different ant species as well.

Our previous research has shown that *C. formosanus* soldiers exhibited significant differences in their responses to freshly killed ants and whole body extracts of the three ant species used in this current study (Cornelius & Grace, 1994a). The ability of *C. formosanus* to distinguish among different ant species on the basis of semiochemicals could potentially be an adaptive response that allows them to recognize particularly threatening enemies. Soldiers responded aggressively to freshly killed ants and whole body extracts of *P. megacephala* significantly more often than toward *T. simillimum* and *O. glaber*. They also responded aggressively significantly more often toward live *P. megacephala* in one-on-one encounters than to the other two species. The majority of soldiers avoided contact with freshly killed and whole body extracts of *O. glaber*, due to the repellency of its anal gland secretions. In contrast, contact with freshly killed *T. simillimum* elicited no response from *C. formosanus* soldiers in 87% of replicates (Cornelius & Grace, 1994a). In this study, we examined how *C. formosanus* responded to the presence of groups of living ants in a laboratory arena and determined if there were differences in the susceptibility of *C. formosanus* to predation by these ant species and of the ants to termite defenses.

MATERIALS AND METHODS

C. formosanus 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). Termites were collected immediately before their use in laboratory assays. Ant colonies were collected at various locations on the island of Oahu and maintained in the laboratory at ambient conditions (23-25°C) in uncovered 30 by 16 cm plastic boxes. The sides of the boxes were coated with liquid teflon (Fluon, Northern Products, Woonsocket, RI), to prevent ants from escaping. Each box contained a 4.5 cm diameter plastic petri dish 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 which contained small holes in the sides of the container and was positioned upside down in the ant box so that ants could collect water droplets when needed. Each box also contained a cap of a 17 by 100-mm plastic Falcon test tube filled with honey. Freshly killed termites were added to boxes for protein approximately once a week.

Bioassays were performed in a three chambered apparatus consisting of three plastic 15 dram vials (60 by 35 mm diameter), connected by 5 mm diameter tygon tubing, 10 cm in length. Vials were coated with Fluon to prevent ants from escaping. Termites were introduced into the first vial with a ratio of 90 workers: 10 soldiers which approximates the natural caste distribution observed in the field (Haverty 1977). Worker ants were introduced into the third vial. Only minor workers of *P. megacephala* were used because minor workers are more likely to engage in foraging activities, whereas major workers are more likely to remain near the nest. A clamp was placed on the tube connecting the second and third vial so that termites and ants remained separated until the experiment began. Termites were introduced several hours before the experiment was started so that they were already moving between the first and second vial before the clamps were removed. The first vial contained 5g of moist sand and the second vial contained a 2.3 cm diameter Whatman No 3 filter paper disk as a food source for termites. The third vial contained cotton soaked in honey water for the ants. In the first experiment, we added 20 ants to each apparatus and we used termites from a single colony. There were 8-10 replicates for each ant species (100 termites per replicate). In the second experiment, we added 50 ants to each apparatus and we used groups of termites from three colonies, 10 replicates from each termite colony and 30

replicates for each ant species.

After ants were added to the third vial of each apparatus, the clamp was removed. In the first experiment, we recorded the number of termite workers and soldiers that were killed or maimed (unable to walk) after 24 hours. In the second experiment, in addition to termite workers and soldiers, we also recorded the number of ants that were killed or maimed. The data were transformed by the arcsine of the square root, blocked by colony in the second experiment, and subjected to analysis of variance (ANOVA) using the general linear models procedure. Means were separated by Tukey's Studentized Range test, $p = 0.05$ (SAS Institute, 1987).

RESULTS

In the first experiment, termite worker mortality was uniformly low (<10%) in replicates exposed to all three ant species (Table 1). However, mortality of termite soldiers ranged from 44-73%. There was significantly more termite soldier mortality in replicates exposed to *T. simillimum* than those exposed to the other two ant species (Table 1).

In the second experiment, there were no significant differences in survivorship among termite colonies. Termite worker mortality was significantly greater in replicates exposed to *T. simillimum* than those exposed to the other two ant species, but there was no difference in termite soldier mortality among ant species (Table 1). Mean mortality of soldiers was over 50% in replicates for all three ant species.

Ants of all three species suffered at least 25% mortality. Mortality of *P. megacephala* was significantly greater than mortality of the other two ant species (Table 1). We observed that *P. megacephala* was more likely to attack termites and move into the first and second vials than *T. simillimum* and *O. glaber*.

DISCUSSION

Because ants of these three species rely primarily on rapid recruitment of large numbers of individuals to overcome prey defenses, they are much more likely to attack termites when their numbers are greater. Hence, termite workers were generally able to escape ant attacks when there were only 20 ants. Soldiers are the first line of defense against ant attacks and they experienced high levels of mortality even though ants had very little impact on termite workers.

Anal gland secretions of *O. glaber* are repellent to *C. formosanus* (Cornelius & Grace 1994b; Cornelius & Grace 1995). In this study, we observed that termites would often retreat rapidly upon contact with *O. glaber*. However, despite the repellency of *O. glaber* secretions, *C.*

Table 1. Mean percent (\pm SD) mortality of termites after 24 h of contact with ants. There were 100 termites in each replicate.

Ant Species	Termite Workers	Percent Mortality	
		Termite Soldiers	Ants
Experiment 1 (20 ants added)			
<i>P. megacephala</i>	5.1a \pm 4.3	56.6a \pm 19.4	
<i>O. glaber</i>	3.7a \pm 2.9	43.7a \pm 19.9	
<i>T. simillimum</i>	9.5a \pm 5.9	73.0b \pm 24.5	
Experiment 2 (50 ants added)			
<i>P. megacephala</i>	13.7a \pm 10.4	56.0a \pm 21.4	46.6a \pm 20.2
<i>O. glaber</i>	17.4a \pm 14.5	51.0a \pm 27.7	25.7b \pm 15.1
<i>T. simillimum</i>	27.5b \pm 15.8	63.3a \pm 23.1	28.1b \pm 19.6

For each experiment, means within a column followed by the same letter are not significantly different. Experiment 1: Termite worker: $F = 3.5$, $df = 2$, $P = 0.05$; Termite soldier: $F = 4.3$; $df = 2$; $P = 0.02$. Experiment 2: Termite worker: $F = 4.9$, $df = 4$, $P = 0.0013$; Termite soldier: $F = 2.3$; $df = 4$; $P = 0.06$; Ants: $F = 5.7$, $df = 4$, $P = 0.0004$

formosanus soldiers still engaged in combat with these ants in their attempt to block tunnel entrances and therefore *O. glaber* caused 44% and 51% mortality of soldiers in the first and second experiments, respectively.

T. simillimum caused significantly greater mortality of termite soldiers in the first experiment and of termite workers in the second experiment. We observed that termites were less likely to retreat upon contact with *T. simillimum* than with the other two ant species and therefore were more likely to encounter *T. simillimum*. In replicates exposed to *T. simillimum*, termite workers would often enter the third vial without becoming disturbed by the presence of ants until they were attacked, whereas termite workers generally did not enter the third vial in replicates exposed to the other two species.

Longhurst *et al.* (1978a) found that termite workers were repelled by the mandibular gland components of ants from several different genera, but not by species which were specialized or semi-specialized termite predators. They hypothesized that specialized termite predators rely on chemical crypsis to move freely among termites without disturbing them before the ants attacked. Longhurst *et al.* (1979b) also observed that termites were generally not disturbed by the presence of the specialized termite predator *Decamortium uelense* (Santchi) in their chambers in laboratory assays.

Although *T. simillimum* is not a specialized termite predator, it appeared to be more effective at preying upon termites in this laboratory study because termites did not immediately retreat upon contact with these ants. In previous research, we found that over 80% of termite soldiers did not respond to freshly killed *T. simillimum*. In contrast, only 36% and 9% of termite soldiers showed no response to freshly killed *P. megacephala* and *O. glaber*, respectively (Cornelius & Grace 1994a). These results are consistent with our observations in this study that *C. formosanus* were less likely to respond to the presence of *T. simillimum* and therefore were more likely to enter a vial containing large numbers of *T. simillimum* where they were more vulnerable to attack by ants.

Interactions among *C. formosanus* and these ant species in Hawaii are the results of recent introductions rather than long-term interactions between sympatric species. Therefore, *C. formosanus* might not recognize *T. simillimum* as a potential predator. *Pheidole* is a widespread genus that contains several species that are known to prey on termites (Hölldobler & Wilson 1990). Thus, termite soldiers might have responded more aggressively to semiochemicals of *P. megacephala* in our previous study because they were selected to respond to cues shared by congeneric species. It is not known if *T. simillimum* prey upon *C. formosanus* in the field. We have not found *T. simillimum* in our termite traps or observed these ants preying upon termites in the field. In contrast, both *P. megacephala* and *O. glaber* are commonly found occupying termite galleries in our termite traps that are set up at various locations on the island of Oahu. In other research, we found that *P. megacephala* was more likely to invade termite tunnels and penetrate through sand barriers than *O. glaber* (unpublished). Hence, *P. megacephala* may have suffered greater mortality due to its aggressive behavior which increased its likelihood of becoming engaged in combat with termite soldiers.

ACKNOWLEDGMENTS

We are grateful to C. Tome for assistance with termite and ant collections, and to E. Smith for technical assistance. Funding was provided by USDA-ARS Specific Cooperative Agreement 58-6615-4-037. This is Journal Series No. 4076 of the Hawaii Institute of Tropical Agriculture and Human Resources.

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