Effect of Termite Soldiers on the Foraging Behavior of *Coptotermes formosanus* (Isoptera: Rhinotermitidae) in the Presence of Predatory Ants

by

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ABSTRACT

The specialized defensive traits of termite soldiers are thought to have evolved largely in response to attacks by ants. Having a greater proportion of soldiers protecting groups of foraging workers could enable termites to expand their foraging areas and enhance their ability to find new food sources. This study examined the effect of *Pheidole megacephala* (F.) (Hymenoptera: Formicidae) on *Coptotermes formosanus* Shiraki foraging behavior, and whether the presence of higher numbers of termite soldiers enabled foraging workers to better withstand ant attacks and maintain access to food sourses. We also examined how differences in soldier proportions affected the construction of new galleries by foraging workers in the absence of ants, and examined whether termites with higher numbers of soldiers moved into new areas faster than than groups with fewer soldiers. In the first experiment, ants completely occupied the foraging tube and blocked termite access to their food source after an average of only 2d for groups with 5% soldiers compared to an average of 6.7d for groups with 20% soldiers. However, there was no evidence that termite groups with 20% soldiers were more likely to explore new areas or construct new foraging galleries faster than groups with only 5% soldiers. Our results indicate that the primary role of *C. formosanus* soldiers in repelling ant attacks against foraging workers appears to be to guard breaks in the tunnel until workers are able to repair the damage.

Key words: Formosan subterranean termite, *Pheidole megacephala*, predation

INTRODUCTION

Termite soldiers are a morphologically distinct caste that are specialized to defend the colony from attack by enemies. Soldiers of the

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Formosan subterranean termite, *Coptotermes formosanus* have enlarged, heavily sclerotized head capsules and mandibles. They rely on mandibular attack and the secretion of a sticky, milky fluid from the fontanelle on their heads as a defense (Mill 1983). In colonies of *C. formosanus*, soldiers comprise between 10-20% of the colony (Haverty 1977). This proportion of soldiers is one of the highest for any social insect (Oster & Wilson 1978). Termite soldiers depend upon workers to feed them and do not contribute to the colony by constructing or repairing galleries. Therefore, soldiers must be making significant contributions to colony defense in order for the colony to maintain such a high number of soldiers at an energetic cost to colony growth.

The specialized defensive traits of termite soldiers are thought to have evolved largely in response to attacks by ants (Traniello 1981, Deligne *et al.* 1981, Mill 1983). However, the most effective method for termites to avoid ant predation is to construct physical barriers of soil, masticated wood, and salivary secretions (Deligne *et al.* 1981). Ants are often unable to break into intact termite galleries. Moreover, exposed termite soldiers are easily overcome by predatory ants (Mill 1983, Waller & La Fage 1987, Cornelius & Grace 1995, 1996). In a previous study (Cornelius & Grace 1996) examining the effect of the big-headed ant *Pheidole megacephala* on groups of termites with different soldier proportions, there was no difference in termite mortality from ant predation on groups of termites with 10%, 5% or 0% soldiers. When termites were confined to sand-filled containers where they could construct galleries in the sand and use these galleries as physical barriers to ant invasion, termite workers were able to survive in containers invaded by ants even in the absence of soldiers. The construction of galleries by *C. formosanus* workers is their most effective method of defense against *P. megacephala* predation.

At the periphery of the gallery system, termite soldiers play a crucial role in defending foraging workers from ant attacks (Traniello 1981). Having a greater proportion of soldiers protecting groups of foraging workers could enable termites to expand their foraging areas and enhance their ability to find new food sources. In laboratory tests, *C. formosanus* was less likely to move into new areas when the number of soldiers present was low (Wells & Henderson 1993). In the present study, we examined the effect of *P. megacephala* on termite foraging behavior and examined whether the presence of higher numbers of termite soldiers enabled foraging workers to better withstand ant attacks and maintain access to food sources. We also examined how differences in soldier proportions affected the construction of new galleries by foraging workers in the absence of ants, and determined whether termites with higher numbers of soldiers moved into new areas faster than groups with fewer soldiers.

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). Termites were collected immediately before their use in laboratory assays. Colonies of the big-headed ant *P. megacephala* were collected on campus and maintained in the laboratory at ambient conditions (23-25°C) in uncovered plastic boxes (30 by 16cm). The sides of the boxes were coated with liquid Teflon (Fluon, Northern Products, Woonsocket, RI) to prevent ants escaping. Each box contained a plastic petri dish (4.5cm 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. A piece of absorbent paper towel soaked in honey-water and placed in a 4.5cm diameter plastic petri dish provided nourishment. They were also provided with adults and pupae of tephritid fruit flies (*Bactrocera dorsalis* Hendel and *Bactrocera cucurbitae* Coquillett) as a source of protein. Ant colonies were comprised of 500 minor and 25 major workers, 1 queen and 0.5g of brood.

In the first experiment, 200 termites were placed in plastic screw top jars (8cm diameter by 10cm high), each containing 300g of silica sand and 60ml 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. Each container was placed in an uncovered plastic box (30 by 16cm). A 10cm length piece of Tygon tubing (1cm diameter) was inserted into the container through a hole near the bottom and a piece of corrugated cardboard (4 by 1cm) was inserted halfway into the container and halfway into the tube in order to increase the likelihood of termites finding the tube entrance quickly. The end of the tube extending out of the termite container and into the surrounding plastic box was set on top of a block of Douglas-fir wood (25 by 25 by 5mm). There were 20 replicate groups of termites comprised of 95% workers and 5% soldiers, and 20 replicates comprised of 80% workers and 20% soldiers. For each treatment, 10 replicates were exposed to ants and 10 replicates were not exposed to ants.

Termites were allowed to acclimate and tunnel in the sand for 10d before experiments began. After 10d, termites had constructed sand barriers at the end of the tubes and were beginning to move sand within into the tubes. In replicates exposed to ants, the plastic box was connected by Tygon tubing to another plastic box containing an ant nest. A rubber stopper placed in one end of the tubing connecting the two boxes prevented ants from entering the second box during the 10d acclimation period. The sides of the boxes were coated with liquid Teflon (Fluon, Northern Products, Woonsocket, RI) to prevent ants from escaping. After 10d, the rubber stopper was removed and ants were allowed to move freely between the two boxes. Observations of ant/termite interactions were made daily for 15d, and the number of days until ants completely occupied the tube connecting the termite container to the wood block was determined for each replicate and compared using a t-test (SAS Institute 1987). Differences in the initial and final oven dry weights of the wood blocks among treatments were subjected to a two-way analysis of variance (ANOVA) using the general linear models procedure (SAS Institute 1987). Proportional termite mortality was transformed by the arcsine of the square root and also subjected to a two-way analysis of variance (ANOVA) using the general linear models procedure (SAS Institute 1987).

In a second experiment, 200 termites were placed in plastic screw top jars (8cm diameter by 10cm high), each containing a block of Douglas-fir wood (25 by 25 by 5mm) on the bottom of the container for food, 200g of silica sand and 40ml 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. Each container was placed in an uncovered plastic box (30 by 16cm). A piece of corrugated cardboard (4 by 1cm) was inserted through a 1cm diameter hole at the base of one side of the container so that half of the cardboard was inside the termite container and the remaining part of the cardboard was in contact with the bottom of the surrounding box. Thus, termites were able to use the cardboard to enter and leave the nest container. Termites began to construct sand galleries from the container along the bottom of the plastic box. Measurements of gallery length were taken daily. There were 10 replicates comprised of 95% workers and 5% soldiers and 10 replicates comprised of 80% workers and 20% soldiers. Total gallery lengths among treatments after 10d and proportional termite mortality (transformed by the arcsine of the square root) were compared using a t-test (SAS Institute 1987).

RESULTS AND DISCUSSION

In the first experiment, ants completely occupied the foraging tube and blocked termite access to their food source after an average of only 2d for replicates with 5% soldiers compared to an average of 6.7d for replicates with 20% soldiers (Table 1). Termite feeding was less for replicates exposed to ants (F=16.98; df=1; p=0.0002), but the amount of wood consumed by these groups was not affected by soldier proportion (F=0.13; df=1; p=0.72) (Table 1). Mortality after 15d was greater in replicates exposed to ants when compared to controls (F=74.68; df=1; p=0.0001), but that mortality was not affected by soldier proportion (F=0.16; df=1; p=0.24). In the second experiment, there was no difference in the time it took for termites with 5% or 20% soldiers to begin constructing new galleries nor in the gallery lengths after 10d (Table 2).

Termite soldiers are not only important in defending the nest against ant attacks, they also play a role in defending foraging workers. Soldiers of *Nasutitermes costalis* function as scouts that discover new food sources and then recruit workers (Traniello 1981). The scouting behavior of *N. costalis* soldiers appears to be a defense against ants. Soldiers of *C. formosanus* are involved in protecting foragers as well. Higher proportions of soldiers are often found with foragers (Delaplane *et al.* 1991). In a laboratory study, Wells & Henderson (1993) found that *C. formosanus* showed less movement into new areas when the proportion of soldiers was low. The unpalatability of *C. formosanus* soldiers to ants may also serve as a deterrent to ant attacks (Waller & La Fage 1987).

In this study, where termites built sand tunnels within Tygon tubing to forage on wood blocks, they were able to maintain access to food

Table 1. Effect of *P. megacephala* on the foraging behavior of groups of 200 *C. formosanus* comprised of 5% or 20% soldiers.

% Termite soldiers	Mean wood wt loss (g)*	Mean % termite mortality (±SD)*	Mean number of days for ants to occupy tubes**
5% (no ants)	0.147 ± 0.10	17.0 ± 5.7	—
20% (no ants)	0.133 ± 0.09	17.0 ± 13.9	—
5% (with ants)	0.019 ± 0.03	92.3 ± 24.2	2.0 ±0.6a
20% (with ants)	0.053 ± 0.06	74.9 ± 40.5	6.7 ± 6.0b

*Treatments compared using a two-way ANOVA (ants soldier proportion, a=0.05) (SAS Institute 1987). Less wood was consumed by replicates exposed to ants (p=0.0002), but the amount of wood consumed was not affected by soldier proportion (p=0.72). Mortality was greater in replicates exposed to ants (p=0.0001), but was not affected by soldier proportion (p=0.24).
**Means differ significantly at the 0.05 level (t-test) (SAS Institute 1987).

Table 2. Foraging gallery construction in the absence of ants by groups of 200 C. formosanus comprised of 5% or 20% soldiers.

% Termite soldiers	Gallery lengths (cm) after 1 d (±SD)[a]	Gallery lengths (cm) after 10 d (±SD)[a]	Mean termite mortality (±SD)[a]
5%	0.56 ± 0.96	6.85 ± 3.56	12.7± 6.0
20%	0.32 ± 0.70	7.95 ± 3.79	13.2± 7.5

[a]Means within each column do not differ significantly at the 0.05 level (t-test) (SAS Institute 1987). Of 10 replicates per treatment, 3 of the groups with 5% soldiers and 2 of the groups with 20% soldiers initiated gallery construction on the first day.

anddefend tunnels against ant invasion longer when the proportion of soldiers was higher. However, although termites with 20% soldiers were able to maintain access to foraging tubes for a longer period of time, soldier proportion did not affect total wood consumption by termites. It may be that the amount of wood consumed by termites in this relatively short-term study may have been too small to detect such differences.

We found no evidence that termite groups with 20% soldiers were more likely to explore new areas or construct new galleries faster than groups with only 5% soldiers. Thus, our results indicate that the primary role of *C. formosanus* soldiers in repelling ant attacks against foraging workers is to guard breaks in the tunnel until workers are able to repair the damage. Once ants occupy a foraging area, both workers and soldiers either retreat or are killed by *P. megacephala*. When *P. megacephala* encounters termites in an exposed situation or is able to break into termite galleries, it kills both termite soldiers and workers (Cornelius & Grace 1996). Therefore, termite soldiers probably make their most significant contribution to the colony by protecting foraging workers from ants at tunnel openings and while tunnels are repaired, thus helping to maintain access to food sources.

Although termite colonies protect themselves against ants primarily by building impenetrable galleries, breaks occur within the gallery system due to environmental disturbances. Also, termites create openings at the periphery of the gallery system to allow alates to emerge and to allow foragers to explore new areas. Termite soldiers congregate at these locations and prevent ants from entering termite galleries. The differential ability of groups of *C. formosanus* with a higher proportion of soldiers to withstand attacks by *P. megacephala* demonstrates that termite soldiers play a vital role in protecting the colony from ant predation. The presence of a high proportion of soldiers is more likely to deter ants for a sufficient period of time that termite workers can repair any damage to galleries.

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