

Behavioral Interactions Between *Aphaenogaster rudis* (Hymenoptera: Formicidae) and *Reticulitermes flavipes* (Isoptera: Rhinotermitidae): The Importance of Physical Barriers

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Abstract Predation pressure from ants is a major driving force in the adaptive evolution of termite defense strategies and termites have evolved elaborate chemical and physical defenses to protect themselves against ants. We examined predator–prey interactions between the woodland ant, *Aphaenogaster rudis* (Emery) and the eastern subterranean termite, *Reticulitermes flavipes* (Kollar), two sympatric species widely distributed throughout deciduous forests in eastern North America. To examine the behavioral interactions between *A. rudis* and *R. flavipes* we used a series of laboratory behavioral assays and predation experiments where *A. rudis* and *R. flavipes* could interact individually or in groups. One-on-one aggression tests revealed that *R. flavipes* are vulnerable to predation by *A. rudis* when individual termite workers or soldiers are exposed to ant attacks in open dishes and 100% of termite workers and soldiers died, even though the soldiers were significantly more aggressive towards the ants. The results of predation experiments where larger ant and termite colony fragments interacted provide experimental evidence for the importance of physical barriers for termite colony defense. In experiments where the termites nested within artificial nests (sand-filled containers), *A. rudis* was aggressive at invading termite nests and inflicted 100% mortality on the termites. In contrast, termite mortality was comparable to controls when termite colonies nested in natural nests comprised of wood blocks. Our results highlight the importance of physical barriers in termite colony defense and suggest that under natural field conditions termites may be less susceptible to attacks by ants when they nest in solid wood, which may offer more structural protection than sand alone.

Keywords Ant–termite interactions · *Aphaenogaster rudis* · predation · predator–prey interactions · *Reticulitermes flavipes*

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Introduction

Ants (Hymenoptera) and termites (Isoptera) have been co-evolving for over 100 million years (Hölldobler and Wilson 1990) and have established a number of relationships ranging from amicable to antagonistic. Peaceful associations between ants and termites may include both termitophilous ants (Wheeler 1936; Higashi and Ito 1989) and myrmecophilous termites (Jaffe et al. 1995; Holt and Greenslade 1979); however, such associations are rare. The great majority of ant–termite interactions are highly antagonistic, with the soft-bodied termites usually losing the battle to the heavily armed and sclerotized ants. Many species of ants prey on termites opportunistically and several ant genera are specialized termite predators (*Leptogenys*, *Termitopone*, and *Megaponera*; e.g. Sheppe 1970; Deligne et al. 1981; Hölldobler and Wilson 1990). In response to predatory attacks termites have evolved elaborate physical and chemical defenses (Deligne et al. 1981; Prestwich 1984). Physical defenses can be delivered by both the soldiers and the workers and often include unusual morphological adaptations such as phragmotic heads for blocking nest entrances, a wide array of mandibular shapes, and autothysis (reviewed in Prestwich 1984). Another notable physical defense is the evolution of the soldier caste itself (Deligne et al. 1981; Mill 1983). Chemical defenses are delivered by the soldiers and may involve equally elaborate morphological and glandular devices that produce an array of defensive chemicals (Prestwich 1984). The behavioral interactions between ants and termites have been examined in laboratory (Cornelius and Grace 1996; Quinet et al. 2005) and field studies (Longhurst et al. 1978; Longhurst et al. 1979; Leponce et al. 1999) and most are described as antagonistic, whereby ants prey on termites. Most ant species appear to be prudent predators and have little impact on the survival of mature termite colonies (Sheppe 1970; Lepage 1981; Darlington 1985); however, some species may significantly reduce termite populations (Longhurst et al. 1979; Collins 1981; Abe and Darlington 1985).

In this study, we examined the behavioral interactions between the woodland ant, *Aphaenogaster rudis* (Emery) and the eastern subterranean termite, *Reticulitermes flavipes* (Kollar). Both species are widely distributed throughout hardwood forests in eastern North America (Lynch 1981; Nutting 1990). *A. rudis* and *R. flavipes* have similar nesting preferences and our field observations indicate that *A. rudis* frequently inhabits logs and tree stumps colonized by *R. flavipes* with apparently little separation between the species. In addition, we have previously shown in laboratory and field experiments that *A. rudis* preys on *R. flavipes* (Buczowski and Bennett 2007). Despite the relative abundance of *A. rudis* and *R. flavipes* and their apparent proximity, little is known about the possible interactions between the two species. To examine the behavioral interactions between *A. rudis* and *R. flavipes* we used a series of laboratory aggression assays and predation experiments where *A. rudis* and *R. flavipes* could interact individually or in groups. Individual interactions included aggression tests between *A. rudis* workers and *R. flavipes* workers or soldiers in one-on-one fights in a neutral arena. Group interactions were predation experiments where colony fragments of *A. rudis* and *R. flavipes* could interact in a common foraging arena. Previous laboratory studies that examined the aggressive interactions between predatory ants and termites provided the termites with an

artificial nest, usually a sand-filled container (Cornelius and Grace 1996; Cornelius and Grace 1997; Wells and Henderson 1993). However, such nests may give the ants an unfair advantage and overestimate the effect of ants on the termites. To address this issue, we compared the defensive ability of termite colonies in assays that utilized either an artificial nest (sand-filled container) or a natural nest (pieces of wood colonized by termites).

Materials and Methods

Collection and Maintenance of Insect Colonies

Colonies of the woodland ant, *A. rudis* (Emery) and the eastern subterranean termite, *R. flavipes* (Kollar) were collected in a mature beech–oak–hickory forest at the Horticulture Park on the campus of Purdue University, West Lafayette, IN. Ant colonies collected from rotting logs were established in Fluon™-coated plastic trays provided with a moist plaster nest. Ant specimens were identified based on worker external morphology (Creighton 1950). Subsequently, colonies were maintained in debris-free trays and reared on 20% sucrose solution ad libitum, crickets, and artificial diet (Bhatkar and Whitcomb 1970) twice a week. Colonies were maintained at $25 \pm 2^\circ\text{C}$, $60 \pm 10\%$ RH, and 14:10 L:D cycle. Termite colonies were collected from cardboard-baited traps buried next to logs harboring termites. Colonies were brought into the laboratory and allowed to migrate into plastic containers with cellulose powder, moistened pine wood, and paper towels provided as food and harborage. Species identity was verified by external morphology of soldiers (Nutting 1990). Colonies were maintained at $25 \pm 2^\circ\text{C}$, $>80\%$ RH, and in constant darkness. Water was added to rearing containers as needed.

One-on-One Aggression Tests

To examine the behavioral interactions between *A. rudis* workers and *R. flavipes* workers or soldiers we performed one-on-one aggression tests in a neutral arena (modified from Roulston et al. 2003). A randomly selected termite worker or a soldier was transferred to a plastic, Fluon™-coated dish (25mm Ø, 5mm high) and allowed to acclimate for 1min. Subsequently, an ant worker (the intruder) was added and aggression was scored on a 1–4 scale described by Suarez et al. (1999; 1 = ignore, 2 = avoid, 3 = aggression [lunging, brief bouts of biting and/or pulling], 4 = fighting [prolonged aggression, stinging by the ant]). For each test, we allowed the fighting individuals up to 25 encounters and data were analyzed as the maximum score of 25 encounters (Roulston et al. 2003). Each instance of direct physical contact between the ant and the termite was scored as an encounter. Individuals were not tested in more than one trial. In addition, for each interaction we recorded the initiator of the fight (ant, termite, or both), the use of physical (i.e. biting) or chemical (stinging, ant only) defenses, the outcome of aggressive interactions (injury or death of one or both individuals), the number of interactions to kill and time to kill since 1st interaction. Termites were considered dead if they exhibited symptoms of venom poisoning and were unable to maintain an upright stance. Thirty

aggression tests were conducted between ants and termite workers and thirty between ants and termite soldiers.

Predation Experiment: Artificial Termite Nests

We conducted a predation experiment to examine group interactions between colony fragments of *A. rudis* and *R. flavipes*. We utilized a large arena where the ants could openly forage and invade an artificial termite nest. A queenright ant colony containing 300 workers and approximately 50 mixed brood was placed in 100 by 100 by 5cm high plastic, Fluon™-coated tray and allowed to colonize a Petri dish nest (95mm Ø) placed in one corner of the tray. The outside of the dish was spray painted black to provide darkness and dishes were aired out for several weeks before use in assays. The nest was filled with 10g of moist sand:vermiculite mixture (1:1, v:v) and provided with a 5cm diameter piece of paper towel under which the ants incubated brood. The ants were allowed to acclimate to the nest for 1week while provided with food, as described above. A termite colony consisting of 270 workers and 30 soldiers was introduced at the opposite corner. The termites occupied a nest identical to the one described for the ants. This assured that the ants would not raid termite nests for reasons other than food. Before introduction into the ant colony, the termites were allowed to acclimate to the nest for 2days and create galleries in the sand. A single hole (3mm Ø, above sand level) drilled in the side of the dish allowed the ants access to the termite colony. The ants and the termites were allowed to interact for 2days in the presence of alternative ant food (20% sucrose solution) and the experiment was replicated five times using different ant colonies and termites from a single stock colony. At the end of the experiment, any surviving ants and termites were counted to determine mortality. Experiments with ants and termites in the absence of each other served as controls.

Predation Experiment: Natural Termite Nests

The most effective method for termite colonies to defend against predators is to construct physical barriers of soil, wood particles, and saliva (Deligne et al. 1981). We tested the defensive ability of *R. flavipes* against *A. rudis* in a predation experiment where *R. flavipes* nested in a natural nest constructed by the termites. This is in contrast to the assay above, where the termites nested in an artificial nest comprised of a sand-filled container. To examine interactions between *R. flavipes* and *A. rudis* we used the methods described above. Briefly, a queenright ant colony containing 300 workers and 50 brood was placed in 100 by 100 by 5cm high plastic, Fluon™-coated tray and allowed to colonize a nest placed in a corner of the tray. The ants were allowed to acclimate to the nest for 1week while provided with food, as above. Termite nests were made by placing moist pine blocks (15 by 4 by 2cm high) in termite colonies for several months. The termites colonized the blocks by creating several entry holes into each block and hollowing out the inside. Thus, the blocks appeared mostly intact on the outside, but contained numerous galleries on the inside. The termites were then removed from the infested blocks, so they could be counted. This was accomplished by placing the blocks in a plastic box with moist paper towels. As the blocks dried, the termites vacated the blocks and moved into

the paper towels. The dry blocks were then re-moistened and 270 termite workers and 30 soldiers were allowed to colonize each block. A single block was then placed on a bed of moist sand (1cm high) inside of a plastic container (16 by 16 by 7cm high) provided with a lid. This was designed to protect the blocks from drying out during the experiment and the blocks were moistened as necessary. A hole in the side of the container allowed the ants access to the termite colony. The container was introduced at the opposite corner from the ant nest and the ants and the termites were allowed to interact for 7days in the presence of alternative ant food (20% sucrose solution). The experiment was replicated five times using different ant colonies and termites from a single stock colony. At the end of the experiment, any surviving ants and termites were counted to determine mortality.

Statistical Analysis

Statistical analyses were performed in SAS 8.1 (SAS Institute 2002). Nonparametric one-way ANOVA tests (Kruskal–Wallis test) were performed to examine the influence of termite caste (worker vs. soldiers) on termite aggression and survival in one-on-one interactions with ants. This was accomplished by using the PROC NPAR1WAY procedure. A separate ANOVA test was conducted to determine the significance of species, caste, and nest type on mortality using mean ant and termite numbers. Each ANOVA was followed by the least significant difference (LSD) *t* test to test for significant differences between means. The level of significance was set at $\alpha = 0.05$.

Results

One-on-One Aggression Tests

A summary of behavioral interactions between *A. rudis* and *R. flavipes* is presented in Table 1. The ants were always extremely aggressive toward the termites (average aggression score 4.0 ± 0) and showed an equal propensity to bite and/or sting termite workers and soldiers. The ants won 100% of aggressive encounters with the termites and no ants were ever injured or killed in fights with termite workers or soldiers. Termite workers were largely defenseless and passive in fights with the ants. Only $3 \pm 3\%$ of termite workers initiated fights and only $10 \pm 6\%$ of termite workers defended themselves using physical aggression (biting). The majority of workers were quickly envenomed and no longer able to defend themselves. In comparison to termite workers, termite soldiers were significantly more aggressive toward the ants (average aggression score for termite workers: 1.4 ± 0.2 , termite soldiers: 3.3 ± 0.2 , Kruskal–Wallis test; $\chi^2 = 32.75$, $n = 30$, $P < 0.0001$), able to fight the ants off more effectively (average number of ant–termite interactions to kill a termite worker: 2.3 ± 0.2 , soldier: 4.7 ± 0.5 , $\chi^2 = 9.37$, $n = 30$, $P = 0.0022$), able to stay alive longer (average time to kill a termite worker: 2.3 ± 0.2 s, soldier: 4.7 ± 0.5 s, $\chi^2 = 6.58$, $n = 30$, $P = 0.0103$), more likely to initiate fights with ants (average percent of fights initiated by termite workers: $3 \pm 3\%$, soldiers: $13 \pm 3\%$, $\chi^2 = 7.49$, $n = 30$, $P < 0.0001$), and more likely to use physical aggression toward the ants (average % of

Table 1 Summary of Aggressive Interactions Between *A. rudis* and *R. flavipes* Workers or Soldiers in One-on-One Assays

Observation	Termite workers	Termite soldiers	χ^2	df	P value
Aggression by the ant (average maximum score)	4.0±0.0	4.0±0.0	0	1	NS
Aggression by the termite (average maximum score)	1.4±0.2	3.3±0.2	32.75	1	<0.0001
Number of interactions to kill termite	2.3±0.2	4.7±0.5	9.37	1	0.0022
Time to kill the termite (seconds)	80.4±7.2	104.5±9.1	6.58	1	0.0103
Percentage of fights initiated by ants	97±3%	50±6%	16.94	1	<0.0001
Percentage of fights initiated by termites	3±3%	13±3%	7.49	1	0.0027
Percentage of fights initiated by both	0±0%	37±3%	12.56	1	<0.0001
Percentage of ants injured or killed	0±0%	0±0%	0	1	NS
Percentage of termites injured or killed	100±0%	100±0%	0	1	NS
Percentage of fights with ants using physical aggression	100±0%	100±0%	0	1	NS
Percentage of fights with ants using chemical aggression	97±3%	97±3%	0	1	NS
Percentage of fights with termites using physical aggression	10±6%	77±3%	26.70	1	< 0.0001

Means not significantly different by Kruskal–Wallis test ($P \leq 0.05$)

fights with physical aggression, workers: $10 \pm 6\%$, soldiers: $77 \pm 3\%$, $\chi^2 = 26.70$, $n = 30$, $P < 0.0001$). Despite the defensive behaviors by the soldiers, 100% of soldiers died in interactions with *A. rudis* without inflicting any injury to the ants.

Termite soldiers lost individual fights with ant workers even though the soldiers were slightly larger (average body length for termite soldier: $6.78 \pm 0.1\text{mm}$, ant worker: $6.33 \pm 0.06\text{mm}$, $n = 10$), substantially heavier (average body mass for termite soldier: $5.4 \pm 0.2\text{mg}$, ant worker: $2.2 \pm 0.1\text{mg}$, $n = 10$), and had longer mandibles (average mandible length for termite soldier: $1.04 \pm 0.2\text{mm}$, ant worker: $0.56 \pm 0.02\text{mm}$, $n = 10$).

Predation Experiment: Artificial Termite Nests

Whenever a termite nest was discovered the ants recruited heavily and invaded the entire container. The ants removed layers of sand in order to reach termite galleries located mostly at the bottom of the dish. The ants then broke through the galleries, extracted the termites, and carried them back to the colony. Both termite workers and soldiers were attacked and both castes suffered 100% mortality in 2days (Table 2). In

Table 2 Mean Percentage (\pm SEM) Mortality in *R. flavipes* and *A. rudis* After Competitive Interactions in a Large Arena Provided Either Artificial or Natural Termite Nests

Sample	Artificial nest (%)	Natural nest (%)	Control (%)
<i>A. rudis</i> workers	5±1 ^{a,b}	6±1 ^{a,a}	4±1 ^{a,a}
<i>R. flavipes</i> workers	100±0 ^{a,a}	7±1 ^{b,a}	3±1 ^{b,a}
<i>R. flavipes</i> soldiers	100±0 ^{a,a}	6±2 ^{b,a}	5±2 ^{b,a}

Means followed by the same letter are not significantly different by Tukey’s HSD test ($P \leq 0.05$). First letter indicates within row comparisons, second within column comparisons

contrast, only $3\pm 1\%$ of termite workers and $5\pm 2\%$ of termite soldiers died in a control experiment.

Predation Experiment: Natural Termite Nests

When *R. flavipes* nested in natural nests constructed by the termites they easily repelled attacks by *A. rudis* and mortality of termite workers and soldiers was similar to mortality in the controls (Table 2). Each wood block had on average $21\pm 4\%$ entry holes (range: 12–32) ranging in diameter from 1 to 3 mm. The ants partially excavated sand from under the blocks and deposited it throughout the test arena. However, they did not invade termite nests, even though the majority of entry holes were wide enough to allow entry by the ants. We observed that the termites sealed off the majority of the holes and soldiers and/or workers guarded any remaining open holes.

Discussion

Termite colonies protect themselves against ants with a variety of mechanical and chemical defenses usually delivered by the soldiers (reviewed in Prestwich 1984) or by building galleries inaccessible to predators. Previous studies which examined interactions between termites and ants in laboratory assays reported several general conclusions regarding the outcome of ant–termite interactions: (1) termite soldiers are vital in defending termite colonies (Wells and Henderson 1993), (2) despite being better equipped for defense, termite soldiers may suffer higher mortality relative to termite workers because they are the first line of defense against ant attacks (Cornelius and Grace 1995), (3) significant differences exist in the susceptibility of termites to different predatory ant species and in the susceptibility of ants to termite defenses (Cornelius and Grace 1995), and (4) ants can suffer substantial mortality in interactions with termites (Cornelius and Grace 1995). The results of one-on-one aggression tests indicate that *R. flavipes* are vulnerable to predation by *A. rudis* when individual termites are exposed to ant attacks in open dishes. In one-on-one interactions with *A. rudis*, 100% of termite workers and soldiers died. However, in comparison to termite workers, termite soldiers were significantly more aggressive toward the ants, able to fight the ants off more effectively, able to stay alive longer, more likely to initiate fights with ants, and more likely to use physical aggression. Termite soldiers were also larger, weighed more, and had longer mandibles. Yet despite these substantial size advantages, termite soldiers were always defeated by *A. rudis*, a highly aggressive and efficient predator. This indicates that weight and size alone do not influence the outcome of aggressive interactions between *A. rudis* and *R. flavipes*. We observed that the ants used their stingers, rather than the mandibles to attack the termites and appeared to bite the termites not to inflict injury, but to secure a better grip before injecting venom. Such efficient and highly toxic chemical defense may have allowed the ants to win during interactions with termite soldiers.

The results of predation experiments which utilized larger ant and termite colony fragments provide experimental evidence for the importance of physical barriers for termite colony defense. In experiments where the termites nested within artificial

nests (sand-filled containers) *A. rudis* was aggressive at invading termite nests and inflicted 100% mortality on the termites. In contrast, termite mortality was comparable to controls when termite colonies nested in natural nests comprised of wood blocks. In experiments involving artificial nests, the ants removed layers of sand to expose the galleries, carried the sand outside the nest, killed all termites, and subsequently colonized termite nests. Cornelius and Grace (1996) found that termites suffered 100% mortality regardless of worker to soldier ratio where the ants had completely broken through the termite galleries. In contrast, termite mortality was comparable to controls in containers where there was at least one gallery left intact. It appears therefore that sand can offer some protection, depending on whether or not the ants are able to penetrate the sand barrier. Some ant species appear highly adept at excavating sand barriers and breaking into termite galleries, while others may be unwilling or unable to do so (Cornelius and Grace 1996). Results show that *A. rudis* readily penetrates sand barriers protecting termite colonies and efficiently kills termites that cannot retreat into the safety of a nest. In experiments with natural nests, the termites appeared to defend against the ants without much difficulty even though the ants removed the sand from under the wood blocks and in some cases part of the ant colony appeared to nest under the blocks. The termites utilized two main lines of defense. First, termite soldiers clearly performed the defensive duties and guarded the entry holes. Their mandibles were visible at the entrances when the colony was agitated (air blown over entrance holes) and soldiers could be pulled out of the galleries when they clamped onto a toothpick inserted into an entrance. Second, the termites readily sealed off the majority of entry holes to: (1) defend against possible ant attacks, (2) conserve moisture, and/or (3) reduce the amount of light entering the nest. Only a few holes were maintained open, even though we never observed the termites leaving the nest.

In conclusion, our results highlight the importance of physical barriers in termite colony defense and suggest that under natural field conditions termites may be less susceptible to attacks by ants when they nest in solid wood, which may offer more structural protection than sand alone. Furthermore, we offer a simple methodology for generating termite nests that most likely very closely approximate those constructed by the termites under natural field conditions. Such nests provide the termites with a controlled microenvironment and physical defense (Noirot 1970; Chen et al. 1998). We show that such nests can be easily constructed by allowing the termites to feed on pre-moistened wood blocks of various sizes depending on the experimental needs. Subsequently, the number of termites in the blocks can be easily manipulated by using moisture gradients which the termites readily follow (Green et al. 2005). We believe such nests provide an ecologically relevant alternative to the traditional nests made of sand-filled containers and we recommend researchers use such nests in laboratory studies, especially those that seek to examine ant–termite predatory interactions where physical defense provided by the nest appears critically important.

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