Journal of Insect Behavior, Vol. 13, No. 5, 2000

Interspecific Interactions Between *Coptotermes formosanus* and *Reticulitermes flavipes* (Isoptera: Rhinotermitidae) in Laboratory Bioassays

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Accepted April 28, 2000; revised May 11, 2000

Experiments were conducted to examine competitive interactions between the Formosan subterranean termite, Coptotermes formosanus *Shiraki (FST), and the eastern subterranean termite,* Reticulitermes flavipes *(Kollar) (EST), using groups of termites with different worker:soldier proportions. Experiments were conducted using three connected test chambers: an FST chamber, an unoccupied center chamber, and an EST chamber. When groups of FST were comprised of 20% soldiers versus 2% EST soldiers, only 8% of center chambers were occupied exclusively by EST. When groups of FST were comprised of 10% soldiers versus 1% EST soldiers, 44% of center chambers were occupied exclusively by EST. When the only food source was located in the center chamber, 60% of center chambers were occupied by both species. FST did not completely displace EST in any of these experiments.*

KEY WORDS: *Coptotermes formosanus*; *Reticulitermes flavipes*; Isoptera; competition; species interaction.

INTRODUCTION

Human-caused biological invasions are resulting in species extinction and the loss of biodiversity worldwide (Mooney, 1986). Alien species that successfully invade new ecosystems often reach population levels that far exceed those commonly found in their native ecosystems. Alien species often

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displace native species and disrupt native ecosystems. For instance, invasions by alien ant species, such as the imported fire ant, *Solenopsis invicta* (Buren), and the Argentine ant, *Linepithema humile* (Mayr), have decimated native ant communities (Porter and Savignano, 1990; Vinson, 1994; Ward, 1987).

The Formosan subterranean termite (FST), *Coptotermes formosanus* Shiraki, is native to mainland China (Kistner, 1985), but it has now become established in many tropical and subtropical regions of the world. It was first discovered in the continental United States in the 1960s. It is widely believed to have been introduced in the thousands of tons of wooden military cargo crates and pallets shipped back from Asia after World War II (La Fage, 1985). Because of its large colony size and aggressive foraging behavior, a colony of FST does more damage than single colonies of native subterranean termites (Su, 1996). In Hawaii, FST caused major structural damage to an unprotected home within 6 months and almost-complete destruction within 2 years (Tamashiro, 1984).

Anecdotal evidence indicates that Formosan subterranean termite colonies are able to outcompete colonies of native subterranean termites, *Reticulitermes* spp., in the United States. In field observations of FST and *Reticulitermes* spp., FST appears to have displaced *Reticulitermes* spp. at some sites (La Fage, 1985; Su and Scheffrahn, 1988a). However, FST and *Reticulitermes* spp. continue to coexist in New Orleans, LA, despite the fact that this area is heavily infested with FST. For instance, of 500 monitoring stakes placed in the ground on the campus of the Southern Regional Research Center in New Orleans, 5.6% of stakes were infested by termites within 6 months. FST infested 4.8% of stakes and *Reticulitermes* spp. infested 0.8% of stakes (Osbrink *et al.*, 1999). In addition, in the area surrounding the Southern Regional Research Center campus, seven colonies of FST and eight colonies of the eastern subterranean termite (EST), *Reticulitermes Flaypes* (Kollar), were coexisting, and in some cases, the two species of termites were infesting traps that were less than 10 m apart (Cornelius, unpublished). Although FST is considered to be the predominant and more aggressive species (Su and Scheffrahn, 1988), it does not seem likely that FST colonies will completely displace native subterranean termite colonies. This study examined competitive interactions between FST and EST in laboratory bioassays to simulate the impact of FST on populations and foraging territories of EST.

Termite soliders play an important role in defending the colony against enemies, such as ants (Deligne, 1981). Because termite soldiers are specialized for defense, and do not feed or construct tunnels, they represent an energetic cost to the colony. In colonies of FST, soldiers generally account for approximately 10% of individuals, but soldier proportions among foraging populations of FST have reached as high as 60% (Haverty, 1977; Su and La Fage, 1999). In contrast, soldiers generally account for approximately

1–2% of individuals in colonies of EST (Howard and Haverty, 1980, 1981). Also, soldiers of FST respond more aggressively to disturbance than *Reticulitermes* spp. soldiers (Waller and La Fage, 1987). Having a high soldier proportion may benefit FST colonies by providing them with greater protection against predation by ants (Wells and Henderson, 1993). The greater number and aggressiveness of FST soldiers may also play a role in defending the colony against other termite species. Experiments were conducted using groups of termites with different worker:soldier proportions to determine how differences in the number of soldiers affect interspecific interactions between FST and EST colonies.

MATERIALS AND METHODS

Termite Collection and Maintenance

Termites were collected from field colonies in New Orleans, LA. Termites were collected from 10 FST colonies and 5 EST colonies. Termites were collected using underground bucket traps (Tamashiro *et al.*, 1973). Traps were baited with blocks of spruce, *Picea pungens*, wood. In underground traps occupied by EST, corrugated cardboard rolls were placed in traps in addition to wood blocks. EST were also collected directly from infested trees by placing rolls of moist corrugated cardboard inside of plastic containers with the bottoms removed. An infested tree branch was broken off and the container was immediately placed over the stump of the branch. Termites moved into the moist cardboard rolls. Cardboard rolls were replaced every 2 weeks. Termite colonies were identified to species by using identification keys for soldiers (Scheffrahn and Su, 1994). Voucher specimens of soldiers of each colony are stored in 70% alcohol at the Southern Regional Research Center, New Orleans, LA.

Termites were kept in the laboratory at 22–24°C in 5.6-liter covered plastic boxes containing moist sand and blocks of spruce wood or cardboard rolls until they were used in experiments. Termites were used in experiments within 2 months of being collected.

Experimental Design

Experiments were conducted in the laboratory at 22–24°C, using plastic ant farms (21.0 cm long × 1.0 cm wide × 13.5 cm high) (Uncle Milton Industries, Corsica, CA) as test chambers. Each test chamber (ant farm) contained 100 g of sand (Standard Sand and Silica Company, Davenport, FL), moistened with 20 ml of distilled water, and four pieces of yellow pine, *Pinus* *ponderosa*, wood (10 cm long × 0.1 cm wide × 3.5 cm high). Each replicate was comprised of three connected test chambers: an FST chamber, an unoccupied center chamber, and an EST chamber. There were 500 termites of each species in each replicate. One group of termites in each replicate was fed filter paper dyed with 0.03% Nile Blue A dye (w/w) for 1 week before starting the experiment. In half of the replicates, FST workers were dyed blue, and in the other half of the replicates, EST workers were dyed blue so that workers of the two species could be distinguished.

Termites were placed in the top of test chambers and allowed to acclimate and build tunnels in the sand for 3 days before chambers were connected. Each test chamber had a connector on each side, covered with a plastic cap. Chambers were connected by removing the cap and attaching the ends of a 4-cm length piece of tygon tubing to the connectors of two chambers. A chamber containing a group of FST was connected to an unoccupied chamber, containing moist sand and wood, and a chamber containing a group of EST was connected to the opposite side of the same unoccupied chamber. At the end of each experiment, the number of termites of each species in each chamber was determined. If 10 or more individuals of a species were present in a chamber, the chamber was considered to be occupied by that species.

The following experiments were conducted: (1) 10% FST soldiers versus 1% EST soldiers, (2) 10% FST soldiers versus 2% EST soldiers, (3) 2% FST soldiers versus 2% EST soldiers, (4) 10% FST soldiers versus 10% EST soldiers, (5) 20% FST soldiers versus 2% EST soldiers, and (6) 10% FST soldiers versus 2% EST soldiers. In experiment 6, wood was placed in the center chamber only and termites were placed in their separate chambers and allowed to acclimate for only 1 day before both chambers were connected to the center chamber.

Each experiment lasted for 21 days, except experiment 1, which lasted for 24 days. At least two termite colonies of each species were used in each experiment, except that only a single EST colony was used in experiment 4. Termite colonies of each species used in each experiment are listed in Table I. There were at least 10 replicates for each experiment, except that there were only 6 replicates of experiment 4 (Table I).

Data Analysis

Differences in the survival of each species in each replicate were determined using a Wilcoxon signed rank test for matched pairs (SYSTAT, 1996). Proportional survival data for workers and soldiers of each species (based on initial proportions used for each species) were transformed by the arcsine of

Table I. Termite Colonies Used and Number of Replicates for Experiments with Varying Initial Mixtures of Soldier Percentages of FST and EST

Initial soldier percentages, FST vs EST	Number of replicates	Termite colonies used for each experiment[a]	
		FST	EST
1. 10% vs 1%	16	1 (4), 2 (6), 3 (4), 4 (2)	1 (2), 2 (6), 3 (6), 4 (2)
2. 10% vs 2%	10	1 (3), 8 (2), 9 (2), 10 (3)	2 (2), 3 (4), 4 (2), 5 (2)
3. 2% vs 2%	16	1 (6), 4 (3), 5 (1), 6 (2), 11 (4)	2 (2), 3 (4), 4 (10)
4. 10% vs 10%	6	1 (3), 10 (3)	4 (6)
5. 20% vs 2%	12	1 (3), 6 (2), 10 (3), 11 (4)	3 (3), 4 (6), 5 (3)
6. 10% vs 2%	10	1 (4), 5 (2), 6 (2), 10 (2)	4 (3), 5 (7)

[a]Number of replicates of each colony in parentheses.

the square root and subjected to analysis of variance, using nested General Linear Models, with colony nested under species, and treatment means were separated using the Tukey HSD test (SYSTAT, 1996). Untransformed means are presented in the Results.

RESULTS

Experiment 1 (10% FST Soldiers Versus 1% EST Soldiers)

After 24 days, eight center chambers were occupied exclusively by FST, seven center chambers were occupied exclusively by EST, and one center chamber was occupied by both species (Fig. 1). There were six replicates in which FST had become established in the EST chamber. EST did not become established in any of the FST chambers (Fig. 2). In most replicates, whichever species moved into the center chamber first continued to occupy the center chamber at the end of the experiment.

Mortality of EST was greater than mortality of FST in 12 of the 16 pairs (Table II). There were significant differences in the proportional mortality of workers of the two species and in the worker mortality among FST colonies (species, $F = 12.97$, df = 1, $P = 0.001$; colony, $F = 3.43$, df = 6, $P = 0.01$). FST colony 2 suffered significantly greater mortality than colonies 1 and 3 ($P \leq 0.05$). In two of six replicates, colony 2 suffered a high mortality, possibly due to a fungal infection in their chambers. Survival of colony 2 in the other four replicates was over 60%. Interactions with EST were not likely to be the cause of the higher rate of mortality suffered by colony 2, because there were no observations of movement of EST into areas occupied by colony 2.

There were significant differences in proportional soldier mortality between the two species but not among colonies (species, $F = 15.04$, df = 1, $P = 0.001$; colony, $F = 1.89$, df = 6, $P = 0.12$). In 7 of 16 replicates, all

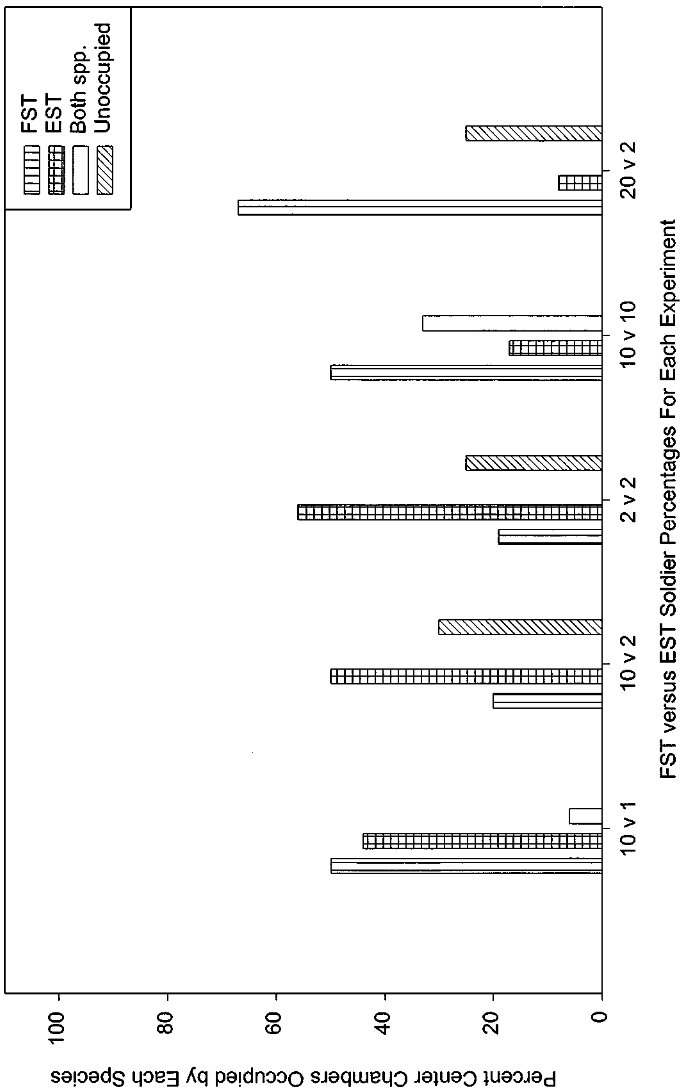

Fig. 1. Percentage of center chambers occupied by each species at the end of each experiment. Soldier percentages of each species in each experiment: 10 v 1, 10% FST versus 1% EST; 10 v 2, 10% FST versus 2% EST; 2 v 2, 2% of both species; 10 v 10, 10% of both species; 20 v 2, 20% FST versus 2% EST. If 10 or more individuals of a species were present in a chamber, the chamber was considered to be occupied by that species.

Table II. Mean (±SE) Number of Termites (Workers + Soldiers) and Percentage of Soldiers Surviving for Experiments with Varying Initial Mixtures of Soldier Percentages of FST and EST[a]

Initial soldier percentages, FST vs EST	Mean + SE number of termites (workers + soldiers) surviving		Percentage soldiers surviving	
	FST	EST	FST	EST
1. 10% vs 1%	409.3 ± 29.7	302.3 ± 28.5*	48.3 ± 6.8	23.8 ± 6.9*
2. 10% vs 2%	368.1 ± 25.7	355.4 ± 22.5	51.6 ± 9.3	40.0 ± 7.6
3. 2% vs 2%	319.5 ± 15.5	302.2 ± 11.9	29.4 ± 9.0	39.4 ± 6.4
4. 10% vs 10%	311.5 ± 51.5	350.8 ± 17.9	38.3 ± 9.4	52.0 ± 8.7
5. 20% vs 2%	288.0 ± 32.9	185.4 ± 43.5	28.8 ± 6.7	5.8 ± 2.9*
6. 10% vs 2% (wood in center chamber only)	305.4 ± 45.4	190.4 ± 36.3	29.0 ± 9.6	22.0 ± 10.2

[a]Significant differences in survival of FST and EST indicated by an asterisk ($P < 0.05$). Termite survival (workers + soldiers) compared using a Wilcoxon signed rank test for matched pairs. Proportional soldier survival data were transformed by the arcsine of the square root and subjected to analysis of variance, using nested General Linear Models, with colony nested under species, and treatment means were separated using the Tukey HSD test. There were 500 termites of each species for each replicate.

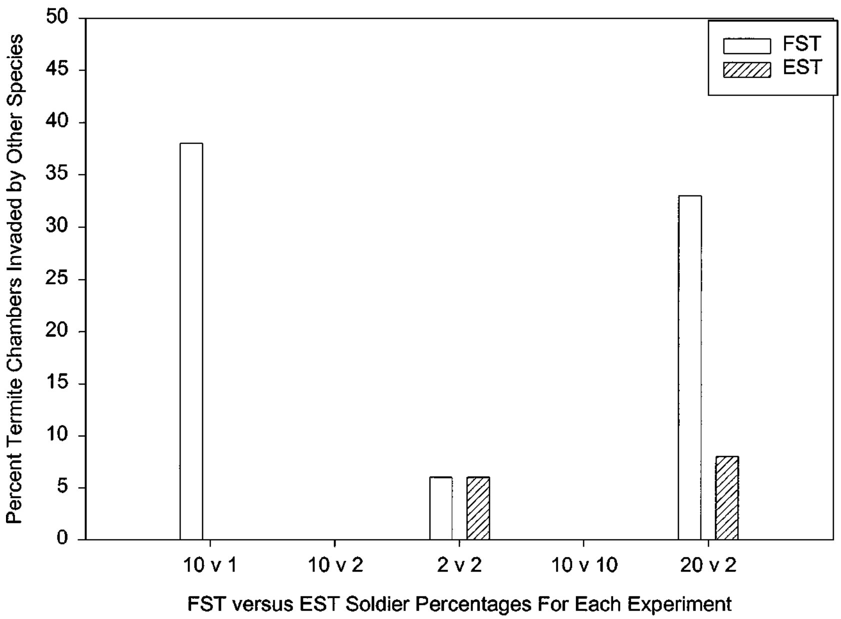

Fig. 2. Percentage of termite chambers for each experiment in which one species occupied the other species' chamber. If 10 or more individuals of a species were present in a chamber, the chamber was considered to be occupied by that species.

five EST soldiers were killed. Survival of FST soldiers varied from 2 to 94%. In all three replicates in which >90% of FST soldiers survived, there were no interactions observed between termite species. EST had initially occupied the center chamber and sealed off the openings connecting the center chamber with the FST chamber. In the six replicates in which FST became established in the EST chamber, survival of FST soldiers was <50%.

Experiment 2 (10% FST Soldiers Versus 2% EST Soldiers)

After 21 days, two center chambers were occupied exclusively by FST, five center chambers were occupied exclusively by EST, and three center chambers were unoccupied (Fig. 1). There were no replicates in which one termite species became established in the other species' chamber (Fig. 2).

There were no significant differences in the overall mortality of FST and EST (Table II). There were no significant differences in the proportional mortality of workers of the two species or among workers of different colonies (species, $F = 0.017$, df $= 1$, $P = 0.90$; colony, $F = 1.85$, df $= 6$, $P = 0.17$). There were no significant differences in the proportional soldier mortality of the two species, but there were significant colony differences in soldier mortality (species, $F = 0.06$, df $= 1$, $P = 0.80$; colony, $F = 7.67$, df $= 6$, $P = 0.001$). FST colony 9 suffered greater soldier mortality than the other three FST colonies. In the two replicates of colony 9, there was 0% survival of FST soldiers. Colony 9 may have suffered greater mortality of soldiers because termites in both replicates moved into center chambers that had previously been occupied by EST.

Experiment 3 (2% FST Soldiers Versus 2% EST Soldiers)

After 21 days, three center chambers were occupied exclusively by FST, nine center chambers were occupied exclusively by EST, and four center chambers were unoccupied (Fig. 1). There was one replicate where FST became established in the EST chamber and one replicate where EST became established in the FST chamber (Fig. 2).

There were no significant differences in the overall mortality of FST and EST (Table II). There were no significant differences in the proportional mortality of workers of different species or colonies (species, $F = 0.55$, df $=$ 1, $P = 0.47$; colony, $F = 0.78$; df $= 6$, $P = 0.60$). There were no significant differences in the proportional mortality of soldiers of the two species, but there were significant differences in soldier mortality among FST colonies (species, $F = 1.79$, df $= 1$, $P = 0.19$; colony, $F = 3.6$, df $= 6$, $P = 0.01$). FST colony 11 suffered greater soldier mortality than colony 1 ($P = 0.027$).

There was 0% survival of colony 11 soldiers in three of the four replicates. In the three replicates where 0% of FST soldiers survived, FST occupied the center chambers, and in one replicate, FST also invaded the EST chamber.

Experiment 4 (10% FST Soldiers Versus 10% EST Soldiers)

After 21 days, three center chambers were occupied exclusively by FST, one center chamber was occupied exclusively by EST, and two center chambers were occupied by both species (Fig. 1). There were no replicates in which one termite species became established in the other species' chamber (Fig. 2).

There were no significant differences in the overall mortality of FST and EST (Table II). There were no significant differences in the proportional mortality of workers of the two species, but there were significant differences in worker mortality among FST colonies (species, $F = 1.82$, df = 1, $P = 0.21$; colony, $F = 45.83$, df = 1, $P = 0.0001$). FST colony 1 workers suffered greater mortality than colony 10 workers ($P = 0.0001$). There were no significant differences in the proportional mortality of soldiers of the two species, but FST colony 1 soldiers suffered slightly greater mortality than colony 10 soldiers (species, $F = 1.66$, df = 1, $P = 0.23$; colony, $F = 5.09$, df = 1, $P = 0.05$).

Experiment 5 (20% FST Soldiers Versus 2% EST Soldiers)

After 21 days, eight center chambers were occupied exclusively by FST, one center chamber was occupied exclusively by EST, and three center chambers were unoccupied (Fig. 1). There were four replicates in which FST became established in the EST chamber and one replicate in which EST became established in the FST chamber (Fig. 2).

There was no significant difference in the overall mortality of FST and EST (Table II). However, the proportional mortality of EST workers ($F = 5.36$, df = 1, $P = 0.034$) and of EST soldiers ($F = 17.79$, df = 1, $P = 0.001$) was significantly greater than the mortality of FST workers and soldiers. There were no significant colony differences in the proportional mortality of workers ($F = 1.32$, df = 6, $P = 0.08$). Soldiers from EST colonies 2 and 3 suffered greater mortality than soldiers from colony 1 of FST ($F = 4.42$, df = 6, $P = 0.008$).

Experiment 6 (Wood in Center Chamber Only)

After 21 days, three center chambers were occupied exclusively by FST, one center chamber was occupied exclusively by EST, and six center

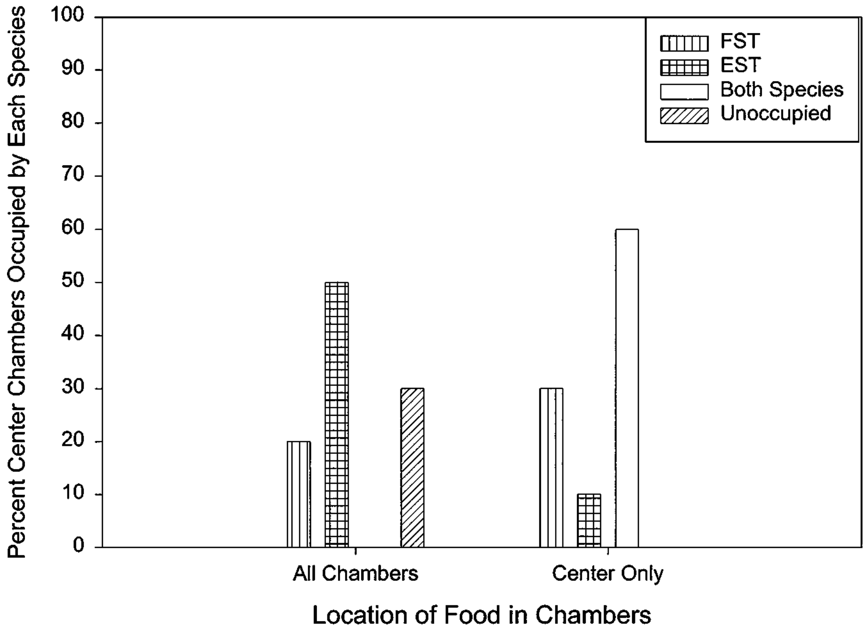

Fig. 3. Percentage of center chambers occupied by each species at the end of the experiment. For both experiments, groups were comprised of 10% FST soldiers and 2% EST soldiers. Location of food in chambers: wood in all three chambers; wood in center chamber only.

chambers were occupied by both species. There was one replicate in which FST became established in the EST chamber. EST did not become established in any of the FST chambers (Fig. 3).

Although the mean number of FST surviving was 305.4, compared with only 190.4 for EST, there was no significant difference in the overall mortality of FST and EST due to the high variability in survival between replicates (Table II). For instance, there were two replicates where one species suffered 100% mortality: FST in one replicate and EST in another replicate. There were no significant differences in the proportional mortality of workers (species, $F = 3.64$, df = 1, $P = 0.08$; colony, $F = 1.46$, df = 4, $P = 0.27$) or soldiers (species, $F = 0.001$, df = 1, $P = 0.98$; colony, $F = 1.99$, df = 4, $P = 0.15$) among species or colonies.

DISCUSSION

Although the Formosan subterranean termite is the predominant subterranean termite species in New Orleans, it has not completely displaced native subterranean termites. In these laboratory bioassays, the two termite species were able to maintain separate foraging territories for 3 weeks without either species being eliminated. EST only suffered significantly greater mortality overall in one of six experiments. In the experiment where the only food source was in the center chamber, FST displaced EST from center chambers in only 3 of 10 replicates, and in 1 replicate, FST suffered 100% mortality. In 60% of replicates, both species became established in the center chamber. The two species avoided interaction by constructing separate tunnels to the wood and sealing off separate feeding areas. Therefore, our results suggest that when foragers of the two species encounter each other in the field, they may be able to avoid each other by establishing separate foraging territories.

In four of six experiments, FST established more foraging territory than EST by taking over a higher percentage of center chambers or by moving from center chambers into EST chambers. Overall, EST occupied FST chambers in only 2 replicates, whereas FST occupied EST chambers in 12 replicates. In the experiment where only the center chamber contained wood, three center chambers were occupied exclusively by FST, compared with only one center chamber occupied exclusively by EST. Because FST seemed to be more aggressive in taking over foraging territory, we predict that FST would have caused significant mortality to EST, especially in experiments 5 and 6, if our experiments had been of a longer duration.

Differences in soldier proportions affected the number of center chambers occupied by each termite species, suggesting that soldiers play an important role in competitive interactions between FST and EST. FST may gain a competitive advantage by having a higher proportion of soldiers because of the combative superiority of soldiers over workers. Chambers (1988) found that soldiers of both species were dominant in one-on-one pairings of soldier versus worker, but neither species was clearly dominant in one-on-one pairings of soldier versus soldier or worker versus worker.

In three experiments, there were significant differences in soldier mortality among FST colonies. In replicates where FST moved into center chambers or invaded the EST chamber, soldier mortality was high. In replicates where FST did not move into other chambers, soldier mortality was low. For example, soldiers from colonies 9 and 11 suffered 100% mortality in replicates where FST moved into areas already occupied by EST. Survival of FST soldiers seemed to be related to the amount of interaction between the two species rather than to differences in the susceptibility of different FST colonies to EST.

Having a high soldier proportion may result in increased movement of foragers into new areas. Differences in the percentage of center chambers occupied by each species were affected not only by the FST:EST soldier ratio, but also by the actual number of FST soldiers present. For instance, two experiments were conducted with a 10:1 FST:EST soldier ratio. When groups were comprised of 20% FST soldiers versus 2% EST soldiers, 67% of center chambers were occupied exclusively by FST and only 8% of center chambers were occupied exclusively by EST. In contrast, when groups of FST were comprised of 10% soldiers versus 1% EST soldiers, 50% of center chambers were occupied exclusively by FST and 44% of center chambers were occupied exclusively by EST. Furthermore, in the two experiments where the FST:EST soldier ratio was 1:1, FST occupied only 19% of center chambers exclusively when groups of both species were comprised of 2% soldiers, and FST occupied 50% of center chambers exclusively when groups of both species were comprised of 10% soldiers. Our results indicate that groups of FST were more likely to move into center chambers when numbers of FST soldiers were high, and less likely to move into center chambers when numbers of FST soldiers were low, regardless of the number of EST soldiers present. Wells and Henderson (1993) found that groups of FST comprised of only 2.4% soldiers were less likely to move into new containers than groups comprised of 18.3% soldiers. Further research is needed to determine how differences in soldier proportions of foraging groups of FST affect their propensity to move into new areas.

A higher soldier proportion may confer an indirect competitive advantage over *Reticulitermes* spp. by providing greater protection against predation. Soldiers play an important role in protecting the colony against predation by ants. In a study comparing predation of groups of FST and *Reticulitermes* spp. with different soldier proportions by fire ants, *S. invicta*, groups of FST suffered less predation than *Reticulitermes* spp when soldier proportions were higher (Wells and Henderson, 1993).

FST may also gain a competitive advantage by having larger populations and foraging territories than *Reticulitermes* spp. In these laboratory bioassays, equal numbers of termites of each species were introduced into chambers. In the field, mature FST colonies are generally thought to be much larger (on average) than mature *Reticulitermes* spp. colonies. Population estimates of FST colonies have ranged from hundreds of thousands to 6.9 million individuals (Su and Scheffrahn, 1988b), whereas population estimates for *Reticulitermes* spp. range from <50,000 to >3 million individuals (Howard *et al.*, 1982; Su *et al.*, 1993; Forschler and Townsend, 1996). Foraging territories measured using mark, release, recapture techniques show that territories of FST extend over an area of 3571 m^2 (Su and Scheffrahn, 1988b), whereas the territories of EST extend over an area of 1091 m^2 (Grace *et al.*, 1989). Therefore, FST colonies may ultimately dominate EST colonies because of their larger populations and foraging territories, as well as their higher soldier proportions.

However, after approximately 50 years of coexistence in the New Orleans area, FST has not completely displaced EST.

ACKNOWLEDGMENTS

We thank Tina Albrecht and Helen Hull-Sanders for their invaluable technical assistance. We also thank Ken Grace, Maureen Wright, Don Daigle, and two anonymous reviewers for constructive comments on early versions of the manuscript.

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