

## Intercolony Aggression in *Reticulitermes flavipes* (Isoptera: Rhinotermitidae)

by

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### ABSTRACT

The relationship between intercolony aggression levels in *Reticulitermes flavipes* and the geographic distance between colony pairings was investigated. The study also examined the relationship between intercolony aggression and intercolony differences in soldier head length and pronotal width. There was a significant difference in the level of aggression demonstrated between colonies found in close proximity to one another (0.1 – 7.9 km), and those found farther apart (8.0 – 60.1 km). Closer colonies were more likely to be passive to one another. Differences in morphological size also yielded significant increases in the amount of aggression displayed between two colonies.

### INTRODUCTION

*Reticulitermes flavipes* (Kollar), the eastern subterranean termite, is one of the most important structural insect pests in the United States (Su & Scheffrahn 1990). It is estimated that termites cost citizens of the United States over \$2 billion annually in damage and control measures (Pinto 1981, Pawson & Gold 1996). The life histories of subterranean termites and their corresponding control techniques, therefore, have received much attention from researchers.

All termite species are classified as eusocial (Thorne 1997). Eusocial insects must demonstrate certain behaviors including nestmate recognition (Wilson 1971). From the conspecific perspective, nestmate recognition allows colony members to direct altruistic behavior in a way that increases their inclusive fitness. From the point-of-view of colony defense, nestmate recognition protects eusocial groups from outside influences that may desire to exploit the colony's resources.

Several researchers have tried to identify the source of cues termites utilize in nestmate recognition. Using a controlled breeding experiment, Adams (1991) concluded that termite recognition cues appear to be inherited. He suggested that this provided evidence that the recognition cues are derived genetically. Other authors suggested that

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environmental influences may play a role in a multiple factor system wherein both environmental and genetic factors affect nestmate recognition (Shelton & Grace 1997). Matsuura (2001) concluded that symbiotic bacteria in the termite hindgut mediate nestmate recognition. The exact mechanism whereby termites distinguish nestmates remains in question.

Intercolony aggression is an ethological tool used to study nestmate recognition in termites (Thorne & Haverty 1991). In aggression studies, it is assumed that colonies that demonstrate antagonistic behavior when paired recognize one another as foreign. Colonies that show no aggressive behavior can not distinguish each other as non-nestmates. Clément (1986) devised a way to quantify recognition based on aggression bioassays.

The present study examined the likelihood that nestmate recognition is based on heritable cues in *Reticulitermes flavipes* (Kollar). This was done by looking at the effect of intercolony physical distance on intercolony aggressive behavior. It was assumed that the closer to one another two colonies are in physical distance the more genetically related they are likely to be (Tobler 1969, Jenkins *et al.* 1998). If recognition is based on heritable cues and if termites demonstrate less antagonistic behavior as their genetic distance decreases, then nestmate recognition may be related to intercolony physical distance.

This study investigated two other heritable factors, intercolony difference in soldier head length and intercolony difference in soldier pronotal width, as predictors of intercolony aggressive behavior. These morphometric measurements are used by isopterists in order to assign individual soldiers in *Reticulitermes* to their species classification (Scheffrahn & Su 1994). There have been reports of the relationship between termite morphology and intercolony agonism, Clément (1978) demonstrated that a correlation existed in European *Reticulitermes* between the presence of nymphs with long wing buds and increased agonism. Husseneder *et al.* (1998) hypothesized that morphological characteristics could play a role in intercolony recognition. Polizzi & Forschler (1999), however, found no relationship between head capsule length and level of antagonism demonstrated by workers in *Reticulitermes* spp.

## MATERIALS AND METHODS

All *R. flavipes* termites used for this study were collected from sites within Brazos, Grimes, and Montgomery Counties, Texas. In all, 24 traps established at 13 different sites were used (Table 1). Sites were chosen based on distance from other sites, presence of termite activity,

and ease of access. Termites were collected using bucket traps as described by Pawson & Gold (1996) or corrugated fiberboard traps as described by La Fage *et al.* (1983). Infested traps were returned to the laboratory and disassembled. From the trap material, termites were extracted and laboratory colonies were established. Species determination was made using averaged morphometric measurements of ten soldiers from each colony. Measurements of head length and pronotal width and labral shape were compared to keys provided by Scheffrahn & Su (1994) and Hostettler *et al.* (1995). All termites used for this study were identified as *R. flavipes*.

Fifty-four pairings were accomplished using colonies located from 0.1 km to 60.1 km apart. Pairings were chosen that would provide an array of distances from all possible pairings. We looked at the amount of antagonistic behavior displayed between colonies found in close proximity (short-distance pairings) compared to the amount of aggression demonstrated by colonies located far apart (long-distance pairings). The descriptors "long-distance" and "short-distance" are relative terms defined within the context of the question and the context of the biology of the organism being studied. For this study, we decided the term "long-distance" would be equated with those distances greater than average alate flight distance. The exact distances, however, that

Table 1. Trap names, trap sites, and their locations for *Reticulitermes flavipes* samples.

Trap Name	Trap Site	Longitude	Latitude
BCC <sub>1</sub>	Brazos County Park	30° 39.945 N	96° 19.102 W
FB <sub>1</sub>	F&B Road	30° 36.639 N	96° 22.256 W
HF <sub>1</sub>	Hall of Fame	30° 38.033 N	96° 22.723 W
HF <sub>2</sub>	Hall of Fame	30° 38.033 N	96° 22.723 W
HWY159 <sub>2</sub>	Highway 159	30° 30.225 N	96° 11.795 W
HWY47 <sub>1</sub>	Highway 47	30° 37.740 N	96° 26.230 W
HWY47 <sub>2</sub>	Highway 47	30° 37.740 N	96° 26.230 W
LC <sub>5</sub>	Lick Creek Park	30° 33.765 N	96° 12.832 W
LC <sub>1-2</sub>	Lick Creek Park	30° 33.765 N	96° 12.832 W
LC <sub>3-2</sub>	Lick Creek Park	30° 33.765 N	96° 12.832 W
LC <sub>5-1</sub>	Lick Creek Park	30° 33.765 N	96° 12.832 W
LC <sub>7-4</sub>	Lick Creek Park	30° 33.765 N	96° 12.832 W
LC <sub>10-2</sub>	Lick Creek Park	30° 33.765 N	96° 12.832 W
LP <sub>4</sub>	Longmire Park	30° 35.676 N	96° 17.837 W
LP <sub>M</sub>	Longmire Park	30° 35.676 N	96° 17.837 W
NB <sub>1</sub>	Navasota Bridge	30° 25.150 N	96° 06.530 W
NF <sub>1</sub>	National Forest	30° 28.568 N	95° 41.089 W
NP <sub>2</sub>	Navasota Park	30° 24.117 N	96° 04.982 W
SC <sub>2</sub>	Sandy Cove	30° 42.220 N	96° 27.060 W
UC <sub>2</sub>	Urban Center	30° 36.897 N	96° 21.083 W
W <sub>2</sub>	Wellborn Road	30° 37.941 N	96° 21.775 W

alates travel during dispersion events is not well understood in *R. flavipes*. In *R. lucifugus*, a closely related species, Grassé (1942) observed distances of a few hundred meters. Other termite species have been shown to fly several kilometers during dispersal (Fuller 1915, Harvey 1934, Grassé 1949). We defined short-distance pairings as those wherein the colonies were found within 7.9 km of one another. Pairs of colonies that were >7.9 km in distance from each other were classified as long-distance pairings. Since the maximum dispersion distance of *R. flavipes* is unknown, the distance threshold of 7.9 km was determined by calculating the median of distances for all 54 pairings. The upper half of the median point was designated as long-distances and the lower half as short-distances. Distances were determined using coordinates taken from a handheld Magellan GPS 315 receiver and ExpertGPS software (TopoGrafix) (Table 1).

The level of aggression demonstrated between two colonies was determined using the protocol established by Clément (1986). All pairings for both studies took place in 150 mm diameter x 25 mm covered Petri dishes (LabTek). Petri dishes were lined with Whatman 44 Ashless 125 mm circle filter papers moistened with 2 mL of tap water. In order to maintain a high level of humidity within the colonies, all covered Petri dishes were placed within a plastic shoebox containing a layer of moistened sand covered by a piece of aluminum foil. Upon completion of setup, pairings were maintained in the dark at 28° C for 24 hrs.

The study involved 10,800 termites in 54 pairings. For each pairing, 20 termite workers from each of two colonies were counted out and separated using an aspirator. At initiation, all 40 termites were placed simultaneously onto opposite ends of the moistened filter paper, and the Petri dish was quickly covered and placed in the dark. Each pairing was replicated five times. After 24 hrs each Petri dish was opened and the total number of dead and injured termites were counted. The antagonism level (AG) of each pairing was measured using the following index:

$$AG = 2.5\left(\frac{\bar{M} + \bar{m}}{2}\right)$$

where " $\bar{M}$ " is the mean number of dead termites in the five Petri dishes and " $\bar{m}$ " the mean number of injured workers" (Clément 1986). Individuals missing either both antennae or more than one leg were counted as moribund. Termites found with one antenna or a missing leg were labeled as "injured". From this formula, variation in aggression between two colonies can range from 0 (no antagonism) to 100 (all workers dead). We followed the suggestion by Clément (1986) defining

high levels of aggression as all indexes greater than or equal to 25.

The data were arcsine square-root transformed and a two-tailed *t*-test was run looking for statistical difference in antagonistic behavior between short-distance and long-distance pairings (Microsoft® Corporation 1997). *P*-values less than 0.05 were deemed significant.

Termites used in the geographic distance study were also used to determine if any relationship existed between differences in morphometric measurements of soldiers and the level of aggression demonstrated by their paired natal colonies. Before all pairings, as described previously, 10 soldiers were removed from each colony and placed in 100% ethyl alcohol for storage until measurements could be made.

Measurements of head capsule length and pronotal width were made with a micrometer. Head capsule length, including mandibles, was measured upon severance from the body and placement in a Petri dish with ethyl alcohol. They were observed with an Olympus SZX12 microscope at 12x power. Pronotal width was measured after the pronotum was removed from each soldier. Slide mounts of pronotums were prepared in a euparal medium on 25 x 75 x 1 mm slides (Fisherbrand) and viewed with a Nikon Alphaphot-2 microscope at 4x power. The measurements of the soldiers from each colony were used to calculate the mean soldier head length and pronotal width. Identification to species was done based on soldier labral shape (Hostettler *et al.* 1995).

The differences in soldier head length and pronotal width were calculated for each pairing. Both calculated differences were ranked and divided into two groups based on the median. The upper half of the median was labeled "large-difference" and the lower half "small-difference". The data were arcsine square-root transformed and a two-tailed *t*-test was run looking for statistical difference in antagonistic behavior between large-difference and small-difference pairings (Microsoft® Corporation 1997). *P*-values less than 0.05 were deemed significant. In addition, the head length and pronotal width differences were added together to give an overall morphological difference, which was subjected to similar statistical analysis.

## RESULTS AND DISCUSSION

The geographic distance of the 52 pairings ranged from 0.1 km to 60.1 km with a median distance of 7.9 km (Table 2). The aggression indexes ranged from 0.00 to 96.00 with an average score of 39.50 ± 38.54 (mean ± SD). A relative frequency histogram of the data demonstrates that the data appear to follow a non-normal, bimodal distribution (Fig. 1). The bimodality of the aggression scores suggests that *R.*

Table 2. Colony pairings sorted by geographic distance from one another. Included in the table are the head length difference, pronotal width difference, and aggression index (AG) for each pairing.

Colony 1	Colony 2	Geographic Distance (km)	Head Length Difference (mm)	Pronotal Width Difference (mm)	Total Difference (mm) <sup>1</sup>	AG
LC5E	LC7-4	0.1	0.006	0.060	0.066	0.00
LC5E	LC5-1	0.1	0.083	0.035	0.118	0.00
LC1-2	LC3-2	0.2	0.256	0.116	0.372	60.00
LC3-2	LC5-1	0.2	0.182	0.096	0.278	20.75
LC5-1	LC7-4	0.2	0.089	0.025	0.114	15.75
LC7-4	LC10-2	0.3	0.103	0.008	0.111	19.00
LC1-2	LC5-1	0.4	0.074	0.096	0.170	0.50
LC3-2	LC7-4	0.4	0.271	0.121	0.392	75.50
LC5E	LC10-2	0.4	0.097	0.052	0.149	0.00
LC5-1	LC10-2	0.5	0.014	0.017	0.031	2.00
LC5E	LC1-2	0.5	0.009	0.055	0.064	1.75
LC1-2	LC7-4	0.6	0.015	0.005	0.020	17.25
LC3-2	LC10-2	0.7	0.168	0.113	0.281	31.00
LC1-2	LC10-2	0.9	0.088	0.003	0.091	0.00
HF2A	W2	1.5	0.264	0.096	0.360	77.50
FB1C	UC2	1.9	0.152	0.054	0.206	0.00
W2	UC2	2.2	0.253	0.042	0.295	0.00
FB1	W2	2.5	0.101	0.018	0.119	0.50
HF2A	FB1	2.7	0.163	0.078	0.241	71.25
NB1	NP2	3.1	0.073	0.031	0.104	0.00
HF1	UC2	3.4	0.029	0.048	0.077	91.00
HWY472B	HF2B	5.6	0.336	0.156	0.492	86.25
BCC1	UC2	6.5	0.055	0.012	0.067	0.00
FB1	HWY47T	6.7	0.044	0.078	0.122	0.50
LC1-2	HWY1592	6.8	0.090	0.082	0.172	0.00
LPM	FB1	7.3	0.078	0.018	0.096	73.00
LPM	W2	7.5	0.023	0.036	0.059	61.25
HWY47T	UC2	8.3	0.196	0.102	0.298	0.00
SC2	HWY47T	8.4	0.045	0.036	0.081	35.50
LC5F	LPM	8.7	0.013	0.091	0.104	87.75
LP4	HF2B	8.9	0.174	0.084	0.258	70.75
SC2	HF2B	10.4	0.222	0.126	0.348	70.75
SC2	W2	11.6	0.102	0.024	0.126	96.00
HWY1592	NB1	12.6	0.111	0.003	0.114	89.00
SC2	FB1	12.9	0.001	0.042	0.043	91.00
SC2	UC2	13.7	0.151	0.066	0.217	17.25
LPM	HWY47T	13.9	0.034	0.096	0.130	86.50
UC2	LC1-2	14.4	0.211	0.127	0.338	90.75
LC5F	FB1	15.9	0.065	0.073	0.138	56.50
W2	LC5F	16.2	0.036	0.055	0.091	0.00
HF1	LC5F	17.6	0.246	0.145	0.391	78.75
LC10-2	NB1	18.9	0.109	0.082	0.191	55.75

Table 2. (Cont.) Colony pairings sorted by geographic distance from one another. Included in the table are the head length difference, pronotal width difference, and aggression index (AG) for each pairing.

Colony 1	Colony 2	Geographic Distance (km)	Head Length Difference (mm)	Pronotal Width Difference (mm)	Total Difference (mm) <sup>1</sup>	AG
LPM	SC2	19.0	0.079	0.060	0.139	81.00
HWY1592	UC2	19.3	0.121	0.045	0.166	89.50
W2	HWY1592	21.4	0.132	0.003	0.135	93.25
SC2	LC5F	27.6	0.066	0.031	0.097	0.00
LPM	NP2	29.6	0.075	0.005	0.080	0.00
FB1C	NB1	32.9	0.080	0.012	0.092	0.00
HWY1592	SC2	32.9	0.030	0.021	0.051	0.00
FB1C	NP2	36.0	0.153	0.043	0.196	0.00
NF1	NP2	39.0	0.194	0.011	0.205	95.50
NB1	NF1	41.1	0.121	0.042	0.163	70.25
HWY1592	NF1	49.1	0.010	0.045	0.055	0.00
LPM	NF1	60.1	0.119	0.006	0.125	72.75

<sup>1</sup>Total Difference = Head Length Difference + Pronotal Width Difference

*flavipes* colonies are most likely to express one of two extremes in aggression level when paired with another unrelated colony, either absolute passiveness or complete aggression. Intermediate levels of aggression are less likely.

The mean aggression score for short-distance pairings ( $n = 27$ ) was  $26.10 \pm 33.45$  (mean  $\pm$  SD). The long-distance pairings ( $n = 27$ ) yielded a mean aggression score of  $52.91 \pm 39.20$  (mean  $\pm$  SD). A two-sample *t*-test for differences between the two levels, short-distance and long-distance, was significant ( $P = 0.011$ ;  $t = 2.615$ ;  $df = 52$ ). These results indicate that colonies of *R. flavipes* demonstrate, on average, higher levels of intercolony aggression the farther their geographic distance is from one another. If higher aggression is likely between geographically distant colonies, and if it is assumed that geographic distance has an inverse relationship with genetic distance, it might be concluded that recognition cues have a heritable component. Caution must be applied to this inference, however, since the true factors involved in recognition cues other than genetic distance may correlate well with geographic distance. Colonies that are found large physical distances apart may be subject to different ecological factors that may in turn determine the levels of intercolony aggression.

Several conclusions can be made, however, based on these data. One can conclude that *R. flavipes* termite colonies found in close proximity to one another are less likely to be aggressive. This is problematic for those who use antagonistic behavior to determine the foraging range of

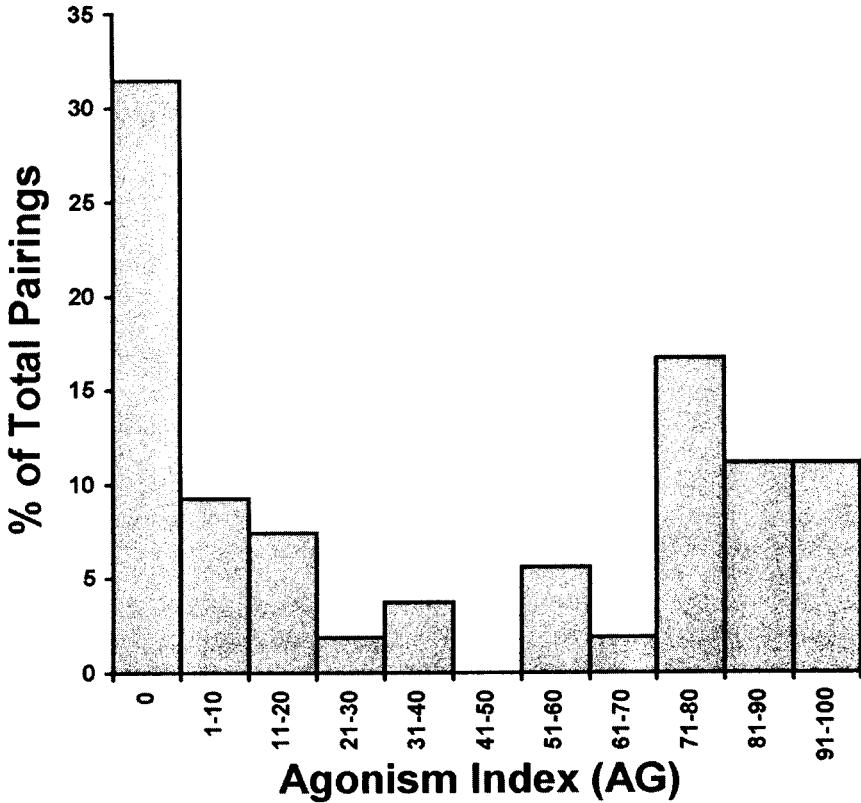


Fig. 1. Percent of pairings demonstrating particular levels of agonism. The data peak at two different points (AG = 0, AG = 71-80), following the pattern of a bimodal distribution.

a colony (Thorne & Haverty 1991). Our data showed that antagonistic behavior was extremely variable. If we use Clément's (1986) threshold index of 25.00 in order to label pairings as "antagonistic" or "non-antagonistic", and we conclude that "non-antagonistic" pairings are from the same colony, then the relatively local pairing LC1-2 vs. LC10-2 would represent a colony with a foraging distance of about 1.0 km. The pairing HWY1592 vs. NF1 would represent a colony with a foraging distance of 49.1 km. This is highly unlikely since data to this point has shown *R. flavipes* colonies to forage no more than 79 m from the main body of the colony (Grace *et al.* 1989, Grace 1990, Su *et al.* 1993, Bulmer & Traniello 2002). Using antagonism to differentiate colonies was only successful 27 out of 54 pairings (50%). It appears that in *R. flavipes*, using antagonism to delineate foraging distance is misleading.

The differences in soldier head length between paired colonies ranged from 0.001 to 0.336 mm. Those grouped under the title "small-



difference" had an average aggression index of  $25.97 \pm 36.26$  (mean  $\pm$  SD). Those head length differences grouped under "large-difference" had an average aggression index of  $52.91 \pm 39.20$  (mean  $\pm$  SD). A two-tailed *t*-test for differences between the two levels, small-difference and large-difference, was significant at  $P = 0.007$  ( $t = 2.80$ ;  $df = 52$ ).

The differences in soldier pronotal width between paired colonies ranged from 0.003 to 0.156 mm. Those grouped under the title "small-difference" had an average aggression index of  $34.13 \pm 39.84$  (mean  $\pm$ SD). Those pronotal width differences grouped under "large-difference" had an average aggression index of  $44.88 \pm 37.16$  (mean  $\pm$  SD). A two-tailed *t*-test for differences between the two levels, small-difference and large-difference, was not significant at  $P = 0.33$  ( $t = 0.97$ ;  $df = 52$ ).

The total morphometric difference (head length difference + pronotal width difference) ranged from 0.02 mm to 0.492 mm. Those grouped under "small-differences" had an average aggression index of  $27.93 \pm 37.67$  (mean  $\pm$  SD). Those with a "large-difference" on average had an aggression index of  $51.08 \pm 36.48$  (mean  $\pm$  SD). A two-tailed *t*-test for differences between the two levels, small-difference and large-difference, was significant at  $P = 0.03$  ( $t = 2.25$ ;  $df = 52$ ); however, these differences were due primarily to head length.

These data indicated that morphological cues are likely not involved in nestmate recognition. A large difference in soldier head length and in the total morphological difference were less likely to be found in colonies demonstrating non-aggressive behavior. The data, however, were extremely variable and unpredictable. For example, the pairings SC2 vs. FB1 and LC5E vs. LC7-4 resulted in similarly little morphological difference between colonies. However, SC2 vs. FB1 resulted in intense aggressive behavior while LC5E vs. LC7-4 demonstrated no antagonism. Likewise, HWY47T vs. UC2 and HWY472B vs. HF2B included colonies with similarly high morphological differences. HWY47T vs. UC2 demonstrated no aggression while HWY472B vs. HF2B resulted in high antagonism (Table 2). Morphological characteristics (at least soldier head length and pronotal width) seem to play no role in intercolony recognition in *R. flavipes*.

We agree that the cues involved in nestmate recognition in *R. flavipes* most likely involve a heritable component (Adams 1991). We demonstrate a relationship between geographic distance (or genetic distance) and intercolony aggression levels. In addition, our study shows correlations between several heritable morphological traits and intercolony antagonism; however, the variability of the data and the lack of predictive power of the studied factors suggests an environmental

influence is involved in recognition mechanisms. This would agree with the "multiple-component hypothesis" (Shelton & Grace 1997). Further research is needed to determine the exact source of the colony specific factors utilized in recognition. The role of and interactions between inheritance and the environment in the expression of those factors would likewise be valuable.

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The name of one of the authors of the following paper was given in error:

Arab, Alberto, Thiago A.O. Pietrobon, Fabio B. Brito, Thalita Rocha, Luceli Santos, Eduardo F. Barbier & Harold G. Fowler 2003. Key to the nest of Brazilian Epiponini Wasps (Vespidae: Polistinae). *Sociobiology* 43(2): 425-432.

The name Luceli Santos should have been Luceli Souza.