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Factors that Affect Aggression Among the Worker Caste of *Reticulitermes* spp. Subterranean Termites (Isoptera: Rhinotermitidae)

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Aggression was observed among both inter- and intraspecific combinations of four colonies of Reticulitermes flavipes *(Kollar) and* Reticulitermes hageni *Banks in laboratory assays each month for 4 consecutive months. Termites were most frequently aggressive toward colonies of a different species. Number of individuals that displayed aggression decreased over the study period, from April to July. There was a slight trend toward reduced aggressive behavior as termites were maintained in the laboratory for 3 months. Passive and aggressive individuals were identified and reexamined for display of aggressive or passive behavior toward nonnestmates. Eighty-nine percent of previously aggressive termites displayed aggression a second time. Eighty-eight percent of previously passive termites were passive upon reexamination. Differences in head capsule size between passive and aggressive individuals provided no correlation between the presence of aggressiveness and the head capsule size in the worker caste.*

KEY WORDS: Isoptera; Rhinotermitidae; *Reticulitermes;* polyethism; agonism.

INTRODUCTION

Agonism is defined as offensive and defensive responses between competing individuals (King, 1973). The presence of aggression and levels of agonistic behaviors can vary among termite species, colonies, and individuals (Thorne, 1982). Previous research with termite agonism indicates that not all pairings from particular colony combinations result in evidence of aggressive encounters

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(Thorne and Haverty, 1991). A correlation between seasonality and aggression has been demonstrated in *Reticulitermes* from southern Europe, with nonnestmates showing reduced agonism during warmer seasons (Clement, 1986). There also is evidence that temites maintained in the laboratory are less likely to display aggression to nonnestmates over time (Nel, 1968; Clement, 1986; Shelton and Grace, 1997).

A division of labor among the termite worker caste in *Reticulitermes*, where only a portion of workers discriminates against nonnestmates through displays of aggression, may also explain equivocal agonism bioassay results (Polizzi and Forschler, 1998). The term polyethism refers to division of labor based on caste, sex, size, and/or age in social insects (McMahan, 1979). The phenomenon of age and its role in the presence of a given behavior in a caste have been studied, with particular attention given to the worker caste in termites (McMahan, 1979). However, studies of temporal polyethism in termites, such as *Reticulitermes*, are complicated because tasks are performed according to caste rather than age and these castes can experience either stationary or regressive molts (McMahan, 1979). Division of labor in the worker caste is more easily defined among species with worker subcastes such as those found in Termitidae (McMahan, 1970; Badertscher *et al.*, 1983; Gerber *et al.*, 1988; Roisin *et al.*, 1990). Roisin *et al.* (1990) stated that older workers of the Termitid *Nasutitermes princeps* performed chores outside the nest, while younger workers performed chores internally. Among the lower termite genera such as *Reticulitermes*, there is a true worker caste (Noirot and Pasteels, 1988). Attempts have been made to distinguish the roles of different-aged workers among lower termites (Howse, 1968; Rosengus and Traniello, 1993; Crosland *et al.*, 1996; McMahan, 1979). Howse (1968) observed that older workers of *Zootermopsis* demonstrated nest building, digging, and oscillatory movements more often than younger workers. However, the possibility of a division of labor, within the termite worker caste, for displays of aggressive behavior has not been tested.

In our examination of *Reticulitermes* behavior toward nonnestmates, we conducted a series of five experiments. The first experiment was designed to initially determine if workers displayed the same level of aggression to nonnestmates inter- or intraspecifically. From these combinations a correlation between month of collection from field colonies and aggression was tested. Second, the effect of maintaining field collected individuals in the laboratory over time on aggression was tested by maintaining individuals for up to 3 months before examining them for aggressive responses toward other colonies. Next, individual termites identified as passive or aggressive from the initial bioassay were retested to determine if their behavior was consistent. If aggressive behavior is relegated to certain workers in *Reticulitermes* colonies, it would be expected that individuals would maintain their aggressive or passive behavior in subsequent bioassays. Differences in head capsule size between passive and aggressive individuals also were tested for a correlation between the presence of aggression and the head capsule size. Size differences may indicate particular instars using the findings of Dyar (1890) and therefore be related to age of the worker. Significant size differences among passive and aggressive individuals could indicate age polyethism in the termite worker caste.

MATERIALS AND METHODS

Termite Collections

Termites were collected from field sites using the techniques of Forschler and Townsend (1996). Termites were removed from four termite monitors, representing four colonies, from Barnesville and Aldora in Lamar County, Georgia, on a monthly basis from March until June. The following field colonies collected from Barnesville were designated I, II, and III. Colony designate IV was collected from Aldora. Colonies I and II colonies were *Reticulitermes flavipes* (Kollar) colonies; III and IV were *Reticulitermes hageni* Banks colonies. Species determination was made using keys to the soldier and alate castes (Weesner, 1964; Scheffrhan and Su, 1994). We chose colonies of these two species because size difference in workers made identification of individuals possible when they were combined in bioassay. In addition, these colonies were used because they provided inter- and intraspecific colony combinations for testing. Termites collected from each of the aforementioned monitors were maintained in separate 9-cm petri plates lined with moistened filter paper that were kept in an environmental chamber at 24°C in total darkness. Individuals were tested within 2 weeks after being collected from field monitors for all tests except for the laboratory conditioning experiment.

Aggression Level Among Individual Workers Based on Monthly Collections

Assay arenas consisted of 6-cm petri plates, lined with filter paper moistened with 0.3 ml distilled water. A pairing consisted of individuals from two colonies placed in the same arena simultaneously. A replication included three termites from each colony, for a total of six termites in a petri plate. Termites were collected prior to inclusion in bioassay by grasping the filter paper to which they were attached and removing them by striking the grasped hand with the other, free hand. Termites would then fall about 10 cm into clean, separate plastic weigh boats. The weigh boats, which contained termites from different colonies, were then tipped over test arenas so that individuals could fall into the arena from a height of 5 cm. This was performed to avoid handling with forceps or aspirators that could cause injury. Three termites from each colony were added to test arenas simultaneously. Only those workers that appeared uninjured, with no missing or injured appendages, were used in bioassay. Each petri plate (replicate) with six termites was observed for 1 h following introduction of termites. Individuals that displayed aggressive behavior such as opening mandibles quickly with the intent to bite (mandible flaring), or biting, were immediately removed with forceps and placed in a separate 3.5-mm arena labeled "aggressive" along with replicate number and colony name. New individuals were added to arenas when aggressors were removed so that three individuals from each colony were present at all times. The clock was reset for 1 h when new individuals were added. If individuals received injuries due to an aggressive encounter, they were removed and discarded, and new individuals added. Termites that did not fight within the 1-h observation time were maintained in the original arena for 24 h. Individuals in arenas where termites were uninjured after 24 h were considered to be passive and were placed into a separate petri plate according to colony and replicate that were labeled "passive." After 24 h, any test arenas with injured individuals were presumed to have aggressors present. Individuals from these arenas were removed from the test because it was impossible to determine the aggressor(s). The aforementioned procedures were repeated for all six colony combinations for each monthly collection, for 4 consecutive months, and replicated 2 to 10 times, depending on the number of termites collected each month. Four or five pairings among nestmates were tested to act as controls during each monthly collection. The number of termites tested varied according to the number that showed aggression and the number collected each month. ANOVA and LSD mean separation techniques were performed on the percentage aggressive individuals to determine which colonies generated the most frequent displays of aggression and to compare the overall aggression of a colony from month to month (SAS Institute, 1990).

Aggression Among Laboratory-Conditioned Termite Workers

Untested termites collected from colonies I, III, and IV, over the 4-month period, were kept in separate 9-cm petri plates lined with moistened filter paper according to collection date. Plates were maintained in an environmental chamber, in complete darkness, at 26°C for 1 to 4 months. Distilled water and moistened filter paper were added when necessary throughout the maintenance period to provide for adequate food and moisture levels.

The steps to test for aggression, described in the previous section, were repeated for this experiment. Data taken from the previous section for these same colony combinations were compared to data from the laboratory conditioned termites taken at monthly intervals. Five arenas, consisting of six nestmates for each colony, were examined, per monthly collection, to provide controls. ANOVA and LSD mean separations of the number of aggressive individuals from each colony were performed for each laboratory conditioning time to compare the percentage of aggressive individuals among colony combinations that were newly collected to those conditioned through 4 months (SAS Institute, 1990).

Recurring Behavior in Workers

Those worker termites previously identified as passive and aggressive were used to test for recurrence of aggression among aggressive or passivity among passive individuals. These bioassays were performed at least 24 h, but no later than 48 h, after an individual's first interaction with a nonnestmate. An individual that was combined with termites from another colony (colony B) in the previous section was always retested with a member of colony B but never tested with the same individuals from the previous test. A replicate consisted of two termites, one from each colony, placed into arenas, using the procedure described previously, and observed for 0.5 h.

Arenas consisted of 17 × 14 × 2-mm (L:W:H) acetate rectangles taped to a 2.5 × 7.6-cm glass microscope slide. Tape was covered with 17 × 14-mm pieces of No. 1 Whatman filter paper, moistened with 0.05 ml of distilled water, and each arena was covered with a glass microscope slide coverslip. The following interactions were tested: both individuals previously aggressive; both individuals previously passive; one individual previously aggressive from colony A and one previously passive from colony B; or vice versa. The term "previously" is used to define the behavior of individuals tested as described in the preceding section, "Aggression Level Among Individual Workers Based on Monthly Collections." Five to ten replications of each interaction and colony combination were observed. A total of 161 previously aggressive termites and 259 previously passive termites was examined. Five pairings among two nestmates of each colony were tested during each collection time for controls. Following the test for recurring behavior, all individuals were preserved in 70% alcohol for later head capsule measurements.

An aggressive individual was defined as any individual that displayed mandible flaring and/or biting. Aggressive individuals were divided into two categories: instigators, or the first individuals to display aggression, and those that displayed aggression in response to being attacked. Passive individuals are defined as those that do not display mandible flaring and biting behaviors. Numbers of aggressive and passive individuals per colony combination and instigators were recorded.

Head Capsule Measurements

Termites preserved in alcohol following the recurring behavior assays were used to take head capsule measurements. Each termite head was excised and placed under a dissecting microscope at a magnification of 38×. Mocha image analysis software was used to take consistent measurements (Jandel

Scientific, 1993). Morphometric measurements were taken for head capsule length—measured from the base of the mandibles to the end of the head capsule; head capsule width—measured from the widest part of the head capsule; and distance between base of both scapes—measured from the inside margins of both scapes. ANOVA and the LSD mean separation technique were used to compare measurements between passive and aggressive individuals (SAS Institute, 1990).

RESULTS

Aggression Level Among Individual Workers Based on Monthly Collections

There was never an indication of aggressive behavior within the nestmate comparisons (controls) from any of the bioassays we conducted. Individuals most frequently displayed aggression, mandible flaring or biting, toward individuals from other species (Table I). Colony III was most frequently aggressive toward interspecific colonies, I and II. However, aggression toward an intraspecific colony, IV, was seen in 11% of the individuals tested. Forty-one and 37% of colony I termites fought with interspecific colonies, III and IV, respectively. None of the colony I termites observed displayed aggression toward colony II, an intraspecific colony. Colony II never displayed aggression toward colony I and always showed aggression toward colony III, but only 25% of their workers showed aggression toward colony IV. Individuals from colony IV showed aggression to all colonies, most frequently colony II, an interspecific colony (Table I).

Table I. Comparison of the Mean Percentage of Aggressive *Reticulitermes* Termite Workers (±SE) by Source Colony from Bioassays Conducted Within 2 Weeks of Collection from the Field by Inter- and Intraspecific Combination, Listed by Colony

Source colony (Species)[a]	Mean percentage aggressive ± SE[b] [n][c]			
	I (Rf)	II (Rf)	III (Rh)	IV (Rh)
When paired with				
I (Rf)	0.0 ± 0 B [18]	0.0 ± 0 B [14]	33.5 ± 6.8 BC [29]	37.0 ± 8.0 AB [27]
II (Rf)	0.0 ± 0 B [14]	0.0 ± 0 B [10]	100.0 ± 0 A [3]	51.8 ± 9.8 A [19]
III (Rh)	37.3 ± 7.4 A [29]	100.0 ± 0 A [3]	0.0 ± 0 D [16]	14.0 ± 4.4 BC [20]
IV (Rh)	41.4 ± 7.8 A [27]	25.0 ± 8.7 B [19]	11.0 ± 4.0 CD [20]	0.0 ± 0 C [18]

[a]Rf, *Reticulitermes flavipes;* Rh, *Reticulitermes hageni.*
[b]Means in the same column followed by the same letter are not significantly different ($P = 0.05$, LSD).
[c]Number of replicates.

The level of aggression toward nonnestmates, for all colonies, decreased significantly from May through June (Table II). Over the 4-month period the percentage of aggressive individuals from colony III fell from 9.1.1 to 10.7%; for colony I, from 96.3 to 10.7%; for colony II, from 52.2 to 8.6%; and for colony IV workers, from 100 to 17.2%. It is possible that the lower number of replicates tested in April for each group may have influenced the percentage of aggressive individuals. However, because the data show that greater than 90% of the individuals tested were aggressive in April, approximately 50% in May and less than 20% in June and July, across all groups tested, we believe that these tests indicate a real trend toward fewer aggressive individuals, not influenced by the number of replicates (Table II).

Table II. Comparison of the Mean Percentage of *Reticulitermes* Worker Termites Displaying Aggression When Combined with Nonnestmates by the Month Termites Were Collected from the Field and Placed in Bioassay Listed by Month and Colony

Month collected	Mean percentage aggressive ± SE[a] (n)[b] in colony No.			
	I	II	III	IV
April	96.3 ± 3.7 A (9)	NTC[c]	91.1 ± 8.9 A (5)	100.0 ± 0 A (4)
May	51.0 ± 14.6 B (20)	52.2 ± 13.8 A (12)	56.7 ± 13.8 B (10)	51.4 ± 10.2 B (20)
June	13.0 ± 5.8 C (21)	0.0 ± 0 B (12)	11.9 ± 7.5 C (14)	16.9 ± 8.2 C (27)
July	10.7 ± 2.8 C (20)	8.6 ± 4.0 B (12)	10.7 ± 2.6 C (23)	17.2 ± 10.2 C (15)

[a]Means in the same column followed by the same letter are not significantly different ($P = 0.05$, LSD).
[b]Number of replicates.
[c]No termites collected.

Aggression Among Laboratory Conditioned Worker Termites

Although termites were maintained under laboratory conditions for 4 months for these tests, the number of workers available for testing at 2 and 4 months allowed for testing only two of the possible six combinations. Therefore, only those months that provided all comparisons are listed in Table III. The results indicate a trend toward reduced percentage of aggressive individuals as the time in the laboratory increased (Table III). The percentage of aggressive individuals in the colony I and colony III combinations provided statisti-

Table III. Comparison of Various Termite Colony Combinations Showing the Mean Percentage of Aggressive Individuals from the Number of Termites Tested by Colony Combination and Length of Time that Termites Were Maintained in the Laboratory Prior to Testing

	Mean percentage aggressive (±SE)[a]					
	Colony III vs		Colony I vs		Colony IV vs	
Month	I	IV	IV	III	I	III
0	33.5 ± 6.8 A	11.0 ± 4.0 A	41.4 ± 7.8 A	37.3 ± 7.4 A	35.8 ± 8.1 A	14.0 ± 4.4 A
1	53.0 ± 3.2 A	6.4 ± 4.1 A	3.1 ± 3.1 B	16.4 ± 8.2 AB	40.0 ± 3.7 A	8.1 ± 5.6 A
3	7.5 ± 3.8 BC	0.0 ± 0 A	16.3 ± 7.8 AB	0.0 ± 0 B	22.0 ± 6.4 AB	5.0 ± 3.3 A

[a]Means in the same column followed by the same letter are not significantly different ($P = 0.05$, LSD).

cally significant reductions in the percentage of aggressive individuals (Table III). However, all combinations showed a trend toward a reduced incidence of aggressive behaviors between newly collected and termite workers maintained in the laboratory for 3 months. These data indicate that maintaining termites in the laboratory for up to 3 months may affect the percentage of aggressive individuals in termite agonism bioassays.

Recurring Behavior in Workers

Data from these tests were combined across colony source and examined by behavior type because we were interested in examining the recurrence of the initial aggressive or passive behaviors exhibited by individual termites when again confronted by a nonnestmate. Termites that displayed aggressive behaviors (mandible flaring and/or biting) were scored as being aggressive. Because one of the two termites would display aggressive behaviors first, we also examined who instigated the aggressive behavior. The termite that did not instigate aggression had two options: (a) it could display avoidance behavior or (b) it could bite and mandible flare in return. As a result, a previously aggressive termite could be termed passive on reexamination if it was attacked and responded only with avoidance behavior. Therefore, a previously passive termite could be listed as aggressive if it responded to an attack by biting in "self-defense."

Previously Aggressive Termites. One hundred forty-three of the 161 (89%) previously aggressive termites displayed aggression when they were again paired with nonnestmates. However, only 2% ($n = 3$) of previously aggressive termites were not involved in an aggressive encounter when resettled and all of these were paired with a previously passive nonnestmate. All other previously aggressive individuals that did not display aggression when retested were paired with individuals that instigated aggressive behaviors. Therefore, 83% (15 of 18) of the previously aggressive termites that did not display aggressive behaviors in the recurrence of behavior bioassay were being attacked and exhibited avoidance rather than aggressive behavior.

Only 40 of the 161 (25%) previously aggressive termites were not instigators of aggression in the second test. From this group of 40 termites, 84% ($n = 34$) were paired with other previously aggressive workers that instigated aggressive behaviors. Eight percent ($n = 3$) of these previously aggressive, noninstigators were paired with previously passive workers that instigated aggression during retesting and the remaining 8% were paired with passive nonnestmates and no aggression occurred.

Previously Passive Termites. Eighty-eight percent (260 of 295 termites) of the previously passive termites remained passive a second time. Of the 35 previously passive termites that displayed aggression, only 3 (9%) instigated battles during the second test. The remaining previously passive noninstigators displayed aggression during the recurrence bioassays only as a result of being attacked. No previously passive termite ever displayed aggression when paired with a previously passive nonnestmate.'

Head Capsule Measurements

There was considerable overlap among passive and aggressive individuals for each head capsule measurement taken for each colony as summarized in Table IV. Significant differences among passive and aggressive individuals were seldom seen (Table IV). Significant differences were predominantly seen in head length (Table IV). However, we believe that these significant statistical differences are of very little biological significance because overlap of head length measurements existed within every measurement category, making predictions based on Dyers rule tenuous.

DISCUSSION

Displays of agonistic behavior are inexorably tied to questions of kin recognition. It is assumed that displays of aggressive behaviors between worker termites is predicated on discrimination of kin and nonkin. Our tests did not attempt to distinguish between more subtle behavioral indications of kin recognition but concentrated only on an overt display of nonkin recognition—aggression. This does not preclude that the worker termites we examined and labeled as nonaggressive did not recognize and distinguish between nestmates and nonnestmates. Our tests simply recorded those termites as nonaggressive. It is entirely possible that scoring bioassays of termite interactions by examining only indications of overt agonistic behaviors overlook more subtle behavioral displays of kin recognition. Therefore, we confine our comments on kin recognition between members of the worker caste in *Reticulitermes* as evidenced by displays of aggression.

Results from these trials were similar to other studies with Rhinotermitidid termites in that aggression is seen predominantly in interspecific pairings and occasionally in intraspecific pairings (Polizzi and Forschler, 1997; Shelton and Grace, 1996, 1997; Clement, 1986). In our tests, the percentage of aggressive individuals steadily declined from month to month but aggressive individuals were present throughout the trials. In June and July we found a significantly lower percentage of aggressive individuals in all colonies compared to those same groups during the March bioassay. Although our sample of months was less than a full calendar year, it does agree with work conducted with several European *Reticulitermes* (Clement, 1986). Clement (1986) suggests that this seasonal aggressive behavior is influenced by genetic relatedness, caste proportions, and availability of food resources.

Other studies observed a decrease in aggression when colonies were main-

Table IV. Mean (±SE), Range, and Number of Termite Worker Head Capsule Measurements (mm) from the Study of Aggressive and Passive *Reticulitermes* Worker Termites

Colony[a]	Head capsule length		Head capsule width		Distance between scapes	
$[n]^b$	Aggressive	Passive	Aggressive	Passive	Aggressive	Passive
I [18 : 15]	1.079 (±0.010) 0.97–1.16	1.055 (±0.022) 0.81–1.13	0.828 (±0.015) 0.65–0.90	0.803 (±0.022) 0.68–0.94	0.731 (±0.009) 0.64–0.78	0.722 (±0.018) 0.55–0.80
II [18 : 19]	1.049 (±0.006) 1.01–1.08	1.040 (±0.008) 0.97–1.09	0.864 (±0.010) 0.76–0.93	0.795 (±0.012) 0.70–0.89	0.707 (±0.008) 0.66–0.74	0.711 (±0.018) 0.67–0.68
III [15 : 13]	0.913 (±0.008) 0.83–0.95	0.891 (±0.005) 0.86–0.92	0.734 (±0.007) 0.68–0.78	0.679 (±0.009) 0.63–0.76	0.627 (±0.004) 0.59–0.68	0.610 (±0.009) 0.57–0.64
IV [32 : 28]	0.867 (±0.005) 0.78–0.95	0.859 (±0.011) 0.71–0.96	0.725 (±0.012) 0.60–0.78	0.686 (±0.010) 0.51–0.79	0.638 (±0.006) 0.55–0.71	0.617 (±0.009) 0.51–0.67

[a]Species of colonies are as follows: I and II, *Reticulitermes flavipes;* III and IV, *Reticulitermes hageni.*
[b]Number of head capsules measured. The first number is the number of aggressive termites; and the second, the number of passive termites.

tained in the laboratory for from 9 months to 10 years (Nel, 1968; Shelton and Grace, 1997). Although our time frame was considerably shorter, our results showed a possible trend toward decreased aggression as termites were maintained in the laboratory for 3 months. Shelton and Grace (1997) demonstrated a lack of agonism among *Coptotermes formosanus* Shiraki colonies that were placed in similar laboratory environments, although they were genetically different and their parental colonies were aggressive. They suggested that exogenous chemical cues from environmental conditioning could be acquired and be an important component in expressing aggressive behavior toward nonnestmates. Their data also suggest that aggressive behaviors could be exacerbated by exogenous cues related to diet or undefined differences in avaiable food resources between field and laboratory-maintained termites.

Our bioassay, retesting individuals for aggressiveness, demonstrated for the first time that aggression is expressed by certain *Reticulitermes* workers and is not a generic, group-related phenomenon. It was observed that not all termite workers fight and those that do are most likely to fight again. Very rarely (3 of 295 individuals, or 1%) did we see previously passive termites instigate battles and never did we see two previously passive nonnestmates display aggression toward one another. Previously passive termites most commonly displayed aggression only after being attacked. These studies demonstrate that all workers are capable of displaying aggression but some termites are more aggressive than others. These data also may indicate a division of labor within the worker caste concerning aggressive behavior.

We tested whether agonism could be an example of temporal polyethism assuming that head capsule size was related to termite worker age. However, termite worker head capsule measurements may not indicate age in *Reticulitermes*. We found no significant differences among head capsule measurements of passive and aggressive individuals (Table IV). These results are similar to those of another study that attempted to distinguish scouts and harvesters of *Reticulitermes flavipes*, where overlapping size ranges were also observed (McMahan, 1979). Miller (1969) states that although *Reticulitermes* workers may molt regularly, after the ninth molt, changes in form are almost undetectable. It is possible that the majority of the individuals we tested had undergone the ninth molt, making head capsule measurements useless in determining age differences. Perhaps aggression in termite workers is not governed by the age of termites. Rosengaus and Traniello (1993) explain that temporal polyethism is usually observed among higher termite species, which typically have large colony populations and high oviposition rates and usually collect food outside the nest. Lower termites, such as *Reticulitermes*, lack these traits that could encourage temporal polyethism (Rosengaus and Traniello, 1993).

It has been demonstrated, through these and other trials, that there is a variety of factors that can affect expression of aggression in worker termites:

the colony, season, and testing conditions (Thorne and Haverty, 1991). Su and Haverty (1991) proposed that recognition cues may be based on combinations of physical and chemical components such as cuticular components, exudates, volatiles, and behavioral and tactile differences. Shelton and Grace (1997) further confirm the possibility of the multiple stimulus hypothesis by demonstrating that more than one cue was probably required in the kin recognition system and that, if all cues are not present, aggression may not occur. Studies have already examined cuticular hydrocarbons among several genera and equivocal data have always been observed where cuticular hydrocarbon phenotypes have and have not been correlated with aggression (Su and Haverty, 1991; Haverty and Thorne, 1989; Takamashi and Gassa, 1995).

However, exogenous cues alone do not explain our results that some individuals are predominately aggressive while others are not. Although early springtime seasonality may have influenced aggression in our tests, it was sometimes overridden when a termite was threatened, as indicated by the passive termites fighting in defense. This suggests that behavioral cues also may be significant. Clement (1981, 1982) has demonstrated the importance of greeting behaviors and variability found among different species of *Reticulitermes* preceding aggression. Greeting behaviors, as well as other behavioral elements, should be studied further to gain a better understanding of the association of the aforementioned cues on expression of passive and aggressive behaviors in individual worker termites. However, it also is possible that displays of aggression could be related to endogenous cues, possibly hormone levels. This could explain those observations of aggressive behavior associated with shifts in caste proportions and removal of individuals from the field into a laboratory situation. Clement (1997) states that to understand kin recognition in termites completely, one must have information concerning the genetics, ethology, and chemistry of termite societies. To this list we would add physiological influences on the expression of aggressive behaviors.

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