

A Review of Intracolony, Intraspecific, and Interspecific Agonism in Termites

by

Barbara L. Thorne¹ & Michael I. Haverty²

ABSTRACT

This review compiles and summarizes approaches and interpretations made to date regarding agonistic behaviors among Isoptera. Laboratory studies of interactions between termites frequently involve placement of test individuals from two colonies into an experimental arena. Direct observations of response, and/or periodic counts of dead or injured termites are scored to assess agonism. Field bioassays, involving position manipulations of individuals or colonies under more natural circumstances, substantiate evidence of intra- or interspecific discrimination among selected termite species.

Reports of aggressive behavior among workers and soldiers from the same parental termite colony are rare and generally attributed to disturbance or injury caused by experimental circumstance. Aggression among or towards reproductives within a nest is known in a number of termite species. Intraspecific termite interactions in some species are passive, but the majority of reports to date describe aggressive responses in encounters between conspecific termite colonies. Such intraspecific agonism has been used as a bioassay to delimit foraging areas of individual colonies. Interspecific aggression in termites appears to be common among sympatric species actively competing for the same food and nesting resources. Agonistic responses in termites often vary depending on individuals, castes, colonies, populations and species involved. In some cases, exogenous conditions such as season, correlate with behavioral patterns.

¹Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA*, and Department of Biology, Northeastern University, Boston, MA 02115, USA

²Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, P.O. Box 245, Berkeley, CA 94701, USA

*Corresponding address.

There is currently no definitive understanding of the recognition/discrimination cues involved in termite-termite behavioral responses. We review suggested stimuli and components which may elicit agonism.

Natural aggressive behaviors between termite colonies might be used constructively in bioassays to learn more about the biology of a particular species, to investigate recognition systems among termites, or to identify natural, biologically active compounds with potential for pre-construction or remedial termite control.

INTRODUCTION

Our knowledge of agonistic behavior among termites remains phenomenological. Central to the study of agonistic behavior in termites is an understanding of competition between termite colonies and an appreciation of the complexities of nestmate recognition in the Isoptera. Different levels of agonistic behavior are involved in securing and maintaining resources, primarily foraging areas. Competitive interactions among functional or potential reproductives within a colony can also result in agonistic behaviors.

Biologists have attempted to evaluate several types of termite-termite interactions, relying largely upon laboratory bioassays. In this paper we will limit the scope of our discussions to termite-termite interactions and exclude discussion of termite aggressive or defensive behaviors in response to other animals. We review the range of methodologies used in studies of agonistic behavior in termites, the variety of agonistic responses observed, and inferences made from these experiments.

The paper commences with discussion of methodologies used in laboratory and then field bioassays of termite-termite interactions. Subsequent sections review data from studies of encounters among nestmates, between individuals from conspecific colonies, and between interspecific groups of termites. Variation in agonistic responses under similar experimental conditions is discussed, followed by a summary of hypotheses and evidence regarding the nature of termite recognition or discrimination cues. Finally, we suggest potential uses of agonistic behavior in the control or management of termite pest species.

LABORATORY BIOASSAYS

There has been no standardization of methodology in bioassays used to examine termite-termite agonistic interactions in the laboratory. The primary goal of these laboratory studies is to make inferences concerning "natural" encounters in the field, but validity of this premise must be studied.

Test Individuals in Experimental Arenas

In almost all cases, experimental interactions to assess aggression are staged between small samples from two termite colonies. From one to several hundred workers and/or soldiers are typically taken directly from the field, or from colonies cultured in the laboratory, and placed in an arena with members of the other test colony. The arenas generally present the termites in a highly artificial, but neutral environment (most commonly a petri dish lined with filter paper; dishes are frequently covered during the experiment). Direct observations of behaviors, and/or periodic counts of dead and injured termites, are scored to assess agonism. In intraspecific encounters, use of dyed termites and video recordings can facilitate detailed observations of behaviors (e.g. Binder 1988, Su and Haverty 1991).

Bouillon (1970) suggests that staged studies showing aggression in termite-termite encounters must be interpreted with caution. He states (p.253), "The observations which have been made regarding the bellicose instincts of termites towards other termites are not significant, because the conditions under which they are made involve a state of stress resulting from the opening of the nest, ... (exposure) to open air, to the introduction into an unfavorable environment, (and)... forced confrontation (with) the 'opponents,' without the built in or ethological barriers which exist in nature."

Levings and Adams (1984) and Adams and Levings (1987) verified results they observed in petri dish arenas by meticulously tracking foraging trails of the *Nasutitermes corniger* (Motschulsky) and *N. nigriceps* (Haldeman) colonies in the field. They found that in all cases in which workers and soldiers collected from different sites fought in assays, careful tracing of foraging trails showed their nests were not connected.

Some investigators have successfully directed encounters under experimental conditions which more closely approximate natural circumstances. Such experimental chambers allow the test termites, removed from their colonies, to habituate in a familiar medium (sand, wood or nest material) before meeting individuals from the other colony.

Nel (1968), for example, placed 40 individuals of *Trinervitermes trinervoides* (Sjöstedt) and *Hodotermes mossambicus* (Hagen) (each group composed of workers and soldiers in "natural" ratios) in opposite sides of a small, square container filled with sand and partitioned in half with a fine mesh copper screen. After a 24 hr "equilibration" period, perturbations were applied (such as removing part of the screen, removing the lid, agitating with a brush) to encourage exploration and thus encounters between colonies.

Howick and Creffield (1980) forced interactions among termites by mixing individuals from different colonies of *Coptotermes acinaciformis* (Froggatt) in single one liter glass jars containing a matrix of vermiculite. Interactions were assessed by comparing wood consumption and survivorship in jars containing mixed vs unmixed colonies.

Working with a *Nasutitermes costalis* (Holmgren) colony acclimated to the laboratory for more than a decade, Traniello and Beshers (1985) were able to introduce a variety of termite species to the test colony in an approximately natural context. Test individuals were placed near *N. costalis* soldiers emerging from the end of a foraging tunnel which had been breached at least one hour prior to testing.

Among a series of experiments on interactions among *Heterotermes aureus* (Snyder) colonies, Binder (1988) simulated foraging encounters by constructing a glass arena with a balsawood barrier separating individuals from two colonies. One group of approximately 500 (both workers and soldiers) was placed on each side of the arena; individuals from one colony were dyed with Sudan Red. The termites were then left to penetrate the barrier, and reaction to the discovery of a competitor colony consuming the same food source was observed with high magnification video recording cameras.

Adams (1991) controlled the presentation of test *Microcerotermes arboreus* Emerson workers by mounting their heads on

thin probes. Head capsules could then be introduced in a "natural" position to specific individuals in the test arena. Before proceeding with the trials, Adams confirmed that hemolymph present on the head capsule, as a result of the decapitation, caused no alarm or avoidance response to other termites.

Entire Colonies

Nel (1968) ran two series of experiments in which four entire laboratory-reared colonies of *Hodotermes mossambicus* (containing reproductives, larvae, workers and soldiers) were introduced, one colony placed in each corner of a pan. The foragers were allowed to explore their new environment and their behavior upon meeting was recorded. In this case, aggressive behavior was limited to "examining;" no termites were physically harmed. Use of entire colonies in interaction experiments is rare, but most realistic in that colony social structure remains intact.

Alternate Bioassay: Soil Barrier Formation

Pearce *et al.* (1990) evaluated the utility of soil barrier formation as an alternate method to direct agonism for distinguishing individuals from different colonies. To investigate intraspecific interactions, they placed 100 major workers of Sudanese *Microtermes* sp. collected from separate bait stations, or distantly collected groups, into petri dishes lined with soil. Three petri dishes (each containing members of a distinct bait-trap origin) were connected together with plastic tubing. The number of entrance holes sealed, partially sealed or not sealed with soil were recorded. In these agonistic bioassays no obvious aggression was observed among *M. lepidus* Sjöstedt workers collected at bait stations within the same general area, but workers collected at different baits frequently produced a total soil seal in the experimental chambers. Such isolation behavior suggests that this species responds to conspecifics from different colonies by formation of a barrier and partitioning off the other group, rather than through overt aggression. *M. lepidus* individuals collected from distant localities did fight, but the alternate bioassay of soil barrier formation proved an effective tool among proximate *M. lepidus* colonies.

Laboratory-Cultured Termites in Bioassays

Several investigators have expressed caution regarding the behavioral responses of termites kept in the laboratory for a prolonged period. Both Nel (1968) with *Hodotermes mossambicus* and Clément (1978) with *Reticulitermes* observed mild to almost non-existent agonism of laboratory colonies when compared with field colonies. Clément (1986) noted that the number of soldiers declines in laboratory colonies of *Reticulitermes*, and that agonism then disappears.

Traniello and Beshers (1985), however, elicited strong fighting and recruitment behaviors from a colony of *Nasutitermes costalis* maintained in the laboratory for ca. 14 years. Laboratory-cultured *Zootermopsis* sp. colonies showed consistent aggressive responses in interspecific interactions (Haverty and Thorne 1989), as did naive soldiers from young colonies reared from alates (Thorne and Haverty 1991). Pearce *et al.* (1990) reared colonies of *Microtermes* sp. nr *lepidus* from alates and evaluated intra-specific encounters after three years. They observed fighting in all intercolony tests.

Clearly, it is prudent to be aware of results which may be artifacts of laboratory rearing. Behavioral patterns should be verified by comparative sampling with individuals recently collected from the field, and if possible, by experiments conducted in the field.

FIELD BIOASSAYS AND EVIDENCE OF DISCRIMINATION

The curiosity of several early investigators resulted in some of the first "studies" of agonistic behavior in termites. Grassi and Sandias (1896-1897) investigated interspecific encounters between *Kaloterms* sp. and *Reticulitermes lucifugus* (Rossi) by placing individuals of one species near the nest entrance or foraging tubes of the other species. Similarly, Dudley and Beaumont (1889) dropped single Panamanian *Nasutitermes* soldiers and workers into established foraging groups of other colonies. Andrews (1911) tested responses among Jamaican *Nasutitermes* by taking termites from one nest and placing them on an alien nest.

Working with *Reticulitermes hesperus* Banks in California, Pickens (1934) inadvertently set up a natural test. He had incipient

colonies in culture (in soil) in a cage which he placed outside for a "more favorable" environment. Pickens reported that workers from resident subterranean colonies explored the cage, discovered and destroyed the incipient colonies.

Andrews (1911), Thorne (1982a) and Levings and Adams (1984) all installed artificial connections or bridges to induce interactions between termites from entire arboreal *Nasutitermes* colonies in the field. In each of these cases workers were recruited to a site where interactions could occur (see also Traniello and Beshers 1985), aggressive battles ensued, and both Thorne (1982a) and Levings and Adams (1984) observed new, diverging construction of foraging systems after these encounters. Levings and Adams (1984) report one case of the death of a small Panamanian *N. nigriceps* colony as a result of an encounter with members of a neighboring *N. corniger* colony.

Direct observations of unmanipulated field evidence of termite agonism are rare. Levings and Adams (1984) and Adams and Levings (1987) reported unmanipulated fights between colonies of *Nasutitermes* in mangroves in Panama. On this same mangrove study area, naturally occurring battles were witnessed between *Nasutitermes nigriceps* and *Termes panamaensis* (Snyder) (E.S. Adams, pers. comm.).

While excavating the passage system of a *Macrotermes michaelseni* (Sjöstedt) colony in a Kenyan savannah, Darlington (1982) found that the passage systems of two closely adjacent *M. michaelseni* nests were connected by several small, weakly constructed passages. Two storage pits in and near these passages were found to contain dry head capsules of termites, and a third storage pit was filled with freshly dead bodies of workers and soldiers. The caste composition present in one pit was representative of caste ratios found in foraging groups of this species. Darlington attributed these "cemetery pits" to the meeting, fighting and withdrawal of foraging parties from neighboring colonies of *M. michaelseni*.

INTERACTIONS AMONG TERMITES WITHIN THE SAME COLONY

Reports of aggressive behavior among workers and soldiers from the same parental termite colony are rare. However, it is known among scientists who study termites that termites will attack

their own nestmates if they are injured first by handling, or by attacks by other termites. If the abdomen of a worker of *Microcerotermes arboreus* is punctured by forceps or if the worker is first injured by a termite from another colony, then it is readily attacked by its own nestmates (E.S. Adams, pers. comm.).

In studies of intercolony encounters the control test of introducing members from the same colony into the experimental arena is standard. Inquisitive behaviors such as antennation are observed, but meetings are generally passive. Even when colonies have been subdivided and kept as isolated populations, docile behaviors are seen when the groups are reunited. Dudley and Beaumont (1889a) separated a portion of a colony of a Panamanian *Nasutitermes* sp., then reintroduced this group after five days. They witnessed no aggressive behavior. Howick and Creffield (1980) isolated parts of a colony of *Coptotermes acinaciformis*, kept these subcolonies in holding jars, then after 28 days reintroduced the subcolonies to colony-mates. These groups were reunited without hostility.

Bouillon (1970) refers to intracolony fighting among soldiers and workers under conditions of disturbance or perturbation, but the species and circumstances involved are not stated. There are scattered reports of cannibalism in termite colonies, but this generally involves consumption of colony-mates which are dead, injured or weakened (reviewed in LaFage and Nutting 1978, see Hendee 1935).

Aggression among or towards reproductives within a nest is known in a number of termites, particularly in the context of elimination of supernumerary reproductives (e.g. Grassé and Noirot 1946, 1960; Lüscher 1952, Grassé 1986). Several researchers have noted that alates will be killed by workers if they do not leave the nest at the appropriate time (Ratcliffe *et al.* 1952, Buchli 1961, Grassé 1986). This topic of reproductive replacement and competition within a colony is complex, and is largely beyond the province of this paper.

INTRASPECIFIC INTERACTIONS

A number of researchers have investigated whether termites effectively discriminate between colony-mates and members of distinct conspecific societies. Observations in this section are

presented roughly chronologically, but once a genus has been introduced, descriptions of congeneric studies follow. Phylogenetic organization of research is deliberately avoided because the species sampled are a haphazard array and no inferences can be drawn about phylogenetic patterns of response.

Passive Encounters

Reports of passive intraspecific encounters are relatively uncommon. These encounters, as defined by Haverty and Thorne (1989, Table II), result in no apparent agonistic reaction, but may involve antennation or mutual grooming or "greeting" with no apparent aversion. Clément (1986) states that intraspecific interactions within *Reticulitermes santonensis* Feytaud are never agonistic. Agonistic behaviors among *Bellicositermes bellicosus* (Smeathman) colonies are reported as absent or weak, with the stated caveat that all tested colonies were collected from the same region (Grassé 1986). Intraspecific aggression is virtually absent in *Zootermopsis nevadensis* subsp. *nevadensis* (Hagen) and in *Z. nevadensis* subsp. *nuttingi* Haverty and Thorne, even when test colonies were collected from geographically disparate areas (Haverty and Thorne 1989). *Z. angusticollis* (Hagen) colonies displayed occasional aggressive or avoidance responses toward one another when the experimental colonies originated from distant localities (Haverty and Thorne 1989). Su and Scheffrahn (1988) and Su and Haverty (1991) observe that *Coptotermes formosanus* Shiraki colonies collected in southern Florida do not fight with each other, while some colonies collected in Hawaii do behave aggressively when they meet.

Thorne (1982a) determined that particular caste combinations in *Amitermes beaumonti* Banks, *Armitermes chagresi* Snyder, and *Nasutitermes corniger* result in intraspecific conflict in certain species while bioassays involving different castes from the same colonies are passive.

Intraspecific Aggressive Interactions

Most literature reports of intraspecific encounters among termites involve displays of immediate and overt recognition

behaviors. Violent agonistic responses, such as attack and dismemberment of intruders by workers, in some cases joined by soldiers, have been reported in a variety of termites.

After dropping one individual into the foraging group of a second Panamanian *Nasutitermes* sp. colony [most likely *N. corniger* and/or *N. ephratae* (Holmgren)], Dudley (in Dudley and Beaumont 1889a, p.96) comments "... had I dropped a miniature dynamite bomb, I could not have caused more confusion."

Studying *Nasutitermes* in Jamaica (probably *N. costalis* because of reference to multiple queens; perhaps involving *N. nigriceps* in some experiments), Andrews (1911) observed workers from one colony attacking workers, soldiers, alates, kings, queens and recently dealated imagoes from a second colony. Intraspecific fighting in *Nasutitermes* (involving both worker and soldier recruitment) has been described in *N. corniger* (Thorne 1982a, Levings and Adams 1984), *N. costalis* (Traniello and Beshers 1985), *N. ephratae* (Thorne 1982a) and *N. nigriceps* (Levings and Adams 1984). Traniello and Beshers (1985) demonstrated that *N. costalis* soldiers are able to distinguish among alien termites, and show a specific response to conspecifics (and also to competitor species) that is characterized by recruitment of large, third instar workers to the point of encounter. The most intense response of *N. costalis* is to alien conspecifics.

Highly aggressive intraspecific responses were observed by Nel (1968) in studies of both *Hodotermes mossambicus* and *Trinervitermes trinervoides*. In the *T. trinervoides* experimental trials, Nel staged caste specific encounters (soldiers vs soldiers, workers vs workers and workers vs soldiers). Soldiers attacked soldiers even in the absence of workers, and workers attacked workers even if no soldiers were present.

Howick and Creffield (1980) inferred high intraspecific interference from experiments involving mixed colonies of *Coptotermes acinaciformis* placed in jars with a piece of wood nesting in a matrix of vermiculite. Both survivorship and the quantity of wood consumed decreased substantially in the mixed colonies compared with unmixed controls. Studying Hawaiian *Coptotermes formosanus*, Su and Tamashiro paired groups of 50 workers from all combinations of each of eight field colonies (reported in Su and Scheffrahn 1988). They observed fighting among many groups, but no fighting

between four of the combinations. Similar experiments involving seven *C. formosanus* colonies from southeastern Florida resulted in no observed intercolonial aggression. Su and Scheffrahn (1988) cited evidence of changes in mean body weights at bait traps and recapture locations of dyed termites to infer fusion of two field colonies of *C. formosanus* in Florida.

In a series of studies of agonism in European *Reticulitermes*, Clément (1978, 1980, 1986) presents a complex pattern of intra-specific interactions. Four species of *Reticulitermes* are considered: *R. santonensis* and *R. (lucifugus) grassei* are sympatric, occurring in humid oceanic climates. *R. (lucifugus) banyulensis* lives in a dry, mediterranean climate; *R. (lucifugus) lucifugus* inhabits humid mediterranean regions. As stated above, *R. santonensis* is always passive in intraspecific encounters (Clément 1986). *R. (l.) banyulensis*, generally monogynous and thus with colonies composed of true siblings (Clément 1986), shows distinct intraspecific agonism (Clément 1980). Aggression within *R. (l.) grassei* and *R. (l.) lucifugus* varies seasonally (Clément 1986). In winter, colonies are "closed", with apparent intraspecific agonism preventing mixing of colonies. Agonism is high during the swarming season. During the summer, societies living in these humid habitats become "open" as agonism decreases. At this season the percentage of neotenics is relatively high in these *Reticulitermes* colonies. In all members of the *R. lucifugus* complex, enzymatic studies suggest that colonies are generally polygynous, although in geographic regions in which the societies are always closed monogyny seems prevalent (Clément 1986). In the northern portion of the distribution of *R. (l.) grassei* there is an exception to this correlation of intracolony genetics and their open or closed nature: colonies of *R. grassei* in the "L1" region are open despite Mendelian frequencies which imply one pair of sexuals per colony.

Preliminary observations made by Thorne, Traniello and Lesniak (unpub. data) show that aggressive fighting can occur between colonies of the eastern subterranean termite, *Reticulitermes flavipes* (Kollar). Workers are the major participants, but soldiers also show aggressive behavior. The same appears to be true of colonies of *Reticulitermes* sp. (probably *R. tumiceps* Banks) from the higher elevations of Arizona (Haverty, unpubl. data).

Binder (1988) conducted a thorough study of intraspecific encounters among *Heterotermes aureus* in Arizona. Using a variety of experimental protocols, he demonstrated marked aggressive behaviors among both paired soldiers and workers and in simulated foraging groups of this desert termite. By immobilizing individuals with a small v-notched card, Binder showed that soldier snaps to a worker's abdomen were less frequent and less aggressive than mandible snaps at the worker's head. In the simulated foraging experiments, paired colonies with equal numbers of soldiers resulted in near decimation of both foraging groups. When one colony had a higher proportion of soldiers, it successfully invaded the colony with fewer soldiers.

In a detailed study of four Sudanese *Microtermes*, Pearce *et al.* (1990) describe a variety of responses to intraspecific encounters. Fighting among workers from different colonies is clear among field samples of *M. sp. nr albopartitus* (Sjöstedt), *M. najdensis* Harris and laboratory reared colonies of *M. sp. nr lepidus* (Sjöstedt). As described above (LABORATORY BIOASSAYS), a soil barrier formation bioassay clearly showed that *M. lepidus* colonies recognize and isolate themselves from one another even though colonies from the same location display no overt aggression. Colonies of *M. lepidus* from distant locations do fight.

Adams (1991) investigated the intraspecific agonistic behavior of *Microcerotermes arboreus* with an innovative bioassay (see section above on LABORATORY BIOASSAYS, Test Individuals in Experimental Arenas). He found that workers of *M. arboreus* were able to distinguish workers of conspecifics on the basis of odors. Furthermore, he was able to demonstrate a genetic component to this behavior; workers were less aggressive toward unfamiliar relatives than toward nonrelatives. He cautions, however, that nestmate recognition is not based solely upon heritable characteristics of individual workers.

Recognition of Larval Termites

In studies of Neotropical *Nasutitermes*, Dudley and Beaumont (1889a,b) and Andrews (1911) report that small, white larval termites lack the discriminatory cues of their mature nestmates,

and are not attacked by alien colonies. Andrews (1911) states that larvae 1 1/3mm long were investigated but not attacked; larvae 2mm long were surrounded and bitten. Sands and Lamb (1975) suggest that this "immunity" of larvae may have implications in deciphering termite recognition cues (see section below on COMPONENTS OF RECOGNITION/ DISCRIMINATION CUES). Additional research on termite responses to alien larvae are needed to evaluate the generality of these behaviors.

Encounters with Alien Reproductives

As a specific objective, or as an unexpected result, some experiments have addressed encounters between worker and soldier termites and functional reproductives from other colonies. Dudley and Beaumont (1889) and Thorne (1982b) introduced physogastric queens into subgroups of alien *Nasutitermes corniger* colonies. The introduced queens were received with apparent tolerance, even in cases in which the recipients had their own primary queen amongst them. This is obviously a totally unnatural experiment, and response is perhaps modified due to common polygyny in this species (Thorne 1982b).

In other, frequently more natural investigations, intraspecific encounters with foreign reproductives have elicited aggression. Pickens (1934) introduced *Reticulitermes hesperus* primary reproductives into a foreign colony and remarked (p. 164) that they were "... immediately set upon by an aroused mob and chewed to a pulp." In his study of incipient colonies, set up in soil in a cage later placed outside, Pickens found that resident workers in the area discovered the cage and destroyed all but a few of the reproductives and workers among his healthy young colonies. Pickens comments (p.164) "This indicates the possible fate of most of those reproductives that attempt to start new colonies in soil already preempted."

Kalshoven (1959) reported that laboratory fusion of young colonies of the Javan termite *Neotermes tectonae* (Dammerman) (reared in small pieces of rotten wood and placed together) results in elimination of one parental couple.

In experiments with *Hodotermes mossambicus*, Nel (1968) observed that an alien reproductive pair dropped into a colony group "deprived" of its own king and queen (duration of primary pair

absence not stated), are frequently seized and killed. However, if the recipient individuals are temporarily kept on one side of the container while the new reproductive pair is introduced along with approximately 50 of their own workers, all are accepted.

Watson *et al.* (1975) noted a tendency for workers of *Mastotermes darwiniensis* Froggatt to destroy alien reproductives in laboratory experiments. Consistency of response varied depending on the type of reproductive, with the greatest tendency toward penultimate stage nymphs and single primary reproductives, and the least tendency toward neotenics.

In colonies of *Zootermopsis angusticollis*, *Z. nevadensis* subsp. *nevadensis* and *Z. nevadensis* subsp. *nuttingi*, introduced alien, functional, conspecific primary or neotenic functional reproductives were killed and consumed by large larvae, nymphs and pseudergates (Haverty and Thorne 1989). This behavior directed toward reproductives contrasts markedly with the generally passive behavior seen among introduced soldiers, nymphs and pseudergates of these species, and likely prevents uncontested fusion of neighboring *Zootermopsis* colonies (Haverty and Thorne 1989).

Encounters Between Reproductives

Nel (1968) investigated interactions among primary reproductives of *Hodotermes mossambicus* collected during a swarming flight and brought into the laboratory. Male versus male, female versus female, and meetings of two male-female pairs were staged in arenas after various periods of isolation of the insects or pairs involved. All combinations showed agonism in the encounters, with aggression tending to increase after 24 hours in isolation, declining again after prolonged isolation (> 273 hrs). Aggression between pairs escalated if they had had a chance to dig into soil before removal for the experiment.

INTERSPECIFIC INTERACTIONS

As with our discussion of intraspecific interactions above, observations in this section are presented chronologically, but once a genus has been introduced, descriptions of congeneric studies follow.

Interactions Among Known Competitors

Termites living sympatrically and using the same resources are potential competitors if the resources are scarce in time and space. Grassi and Sandias (1896-1897) were the first to report interspecific (in this case actually intergeneric) aggression in termites. They placed individual workers of *Reticulitermes lucifugus* (*Termes lucifugus*) into nests of *Kaloterмес* sp. (*Caloterмес*). These species are sympatric in Italy and even occur in the same plant or piece of wood (Springhetti and Amorelli 1982). Grassi and Sandias (1896-1897) observed immediate aggression in their experiment; large larvae and nymphs at once clipped off legs and eviscerated the intruders. When a replacement reproductive of *R. lucifugus* was placed into a *Kaloterмес* nest it was immediately decapitated by a *Kaloterмес* soldier.

Springhetti and Amorelli (1982) and Grassé (1986) examined the agonistic relationship between *Kaloterмес flavicollis* (Fabr.) and *Reticulitermes lucifugus*. When Springhetti and Amorelli (1982) combined pseudergates of each species in the laboratory, the result was mutual aggressiveness. When placed together, these species spend an initial period of 5 to 20 minutes exploring the other species, then they attack. Some of each species survive > 48 hours. Grassé (1986) conducted similar studies with *K. flavicollis* and *R. lucifugus*. When soldiers and larvae of *K. flavicollis* are introduced into a population of *R. lucifugus*, they are rapidly attacked and eaten. However, if *R. lucifugus* individuals are placed into a natural or experimental colony of *K. flavicollis*, the reverse is true: the *R. lucifugus* are quickly dispatched. Grassé cautions that such encounters are unlikely in nature. Even though their galleries occur very close to one another, they never connect. Perhaps recognition behaviors are responsible for this separation.

Bequaert (1913) cites cases of termites occupying portions of the nest of another species. He suggests one species *Coarctotermes* (*Eutermes*) *contractus* (Sjöstedt), may "usurp" another, *Cubiterмес* (*Eutermes*) *pallidiceps* (Sjöstedt), from its own nest, but he provides no direct observations. Likewise, Fuller (1915) implies that *Cubiterмес* (*Eutermes*) *bilobatus* (Haviland) "expels" *Trinerviterмес* (*Eutermes*) *trinervius* (Rambur) from the same nest, but there is no evidence of a fight.

Grassé [1937, cited in Bouillon (1970)] provides several examples of more than one species cohabiting common galleries under bark, in the same runways or in the same nest mound. There appears to be tolerance among these species. Grassé (1986) indicates that even when two species do live in the same nest they usually do not interact in the nest space or foraging galleries. This connotes an avoidance response between species rather than tolerance. Avoidance of *Hodotermes mossambicus* by *Trinervitermes trinervoides* was observed in the laboratory by Nel (1968). If the *T. trinervoides* were "encouraged" to enter the territory of *H. mossambicus*, they were promptly attacked and killed.

Ikehara (1966) found interspecific interactions to be more severe between species which have similar food habits and actually compete for food, than between those having different resource preferences. Similarly, Ikehara (1966) detected increased aggression between species of termites occurring in similar habitats, than those occurring in different habitats. His studies indicated a general hierarchy of dominance among competing, sympatric species.

Bodot (1967) found that termites of the savannas of the Ivory Coast compete for nesting sites regardless of whether they compete for food. *Amitermes evuncifer* Silvestri invades living nests of *Cubitermes severus* Silvestri and *Trinervitermes trinervius* (Rambur). Termitaria of *C. severus* which have a sizable *A. evuncifer* population have an altered nest architecture and an abnormal caste composition. Noirot (1970) illustrated a situation in the savannas of the Ivory Coast in which *A. evuncifer*, *C. severus* and *T. trinervius* produce composite nests. In the subterranean areas of this "nest" *Allognathotermes hypogues* Silvestri, *Promicrotermes holmgreni* (Silvertri) and *Pericapritermes* sp. were also found. Whether "these associations are specific or merely accidental, there is no communication between the systems of galleries of the different species." However, he states that *A. evuncifer* eventually displaces the other species with which it cohabits. Agonistic behavior may play a role in this displacement.

Thorne (1982a), Levings and Adams (1984) and Traniello and Beshers (1985) found species of *Nasutitermes* to be consistently aggressive toward sympatric, competing species. All combinations of species pairs resulted in fighting.

Competition for dead wood and nesting sites is common for two species of dampwood termites, *Zootermopsis angusticollis* and *Z. nevadensis*. These species are sympatric along the Pacific Coast from Baja California north to British Columbia. Colonies of both species are often found in the same piece of wood. Haverty and Thorne (1989) investigated the agonistic relationship between these two species. They found that laboratory pairings of individuals of these two species generally resulted in aggression. Soldier vs. soldier pairings (Fig. 1a) provided the most consistent response; pseudergate vs. pseudergate and soldier vs. three nymphs (Fig. 1b) showed less dramatic aggressive responses. Even naive soldiers of laboratory-reared incipient colonies react aggressively to pigmented larvae, pseudergates and functional reproductives of the opposite species (Thorne and Haverty 1991).

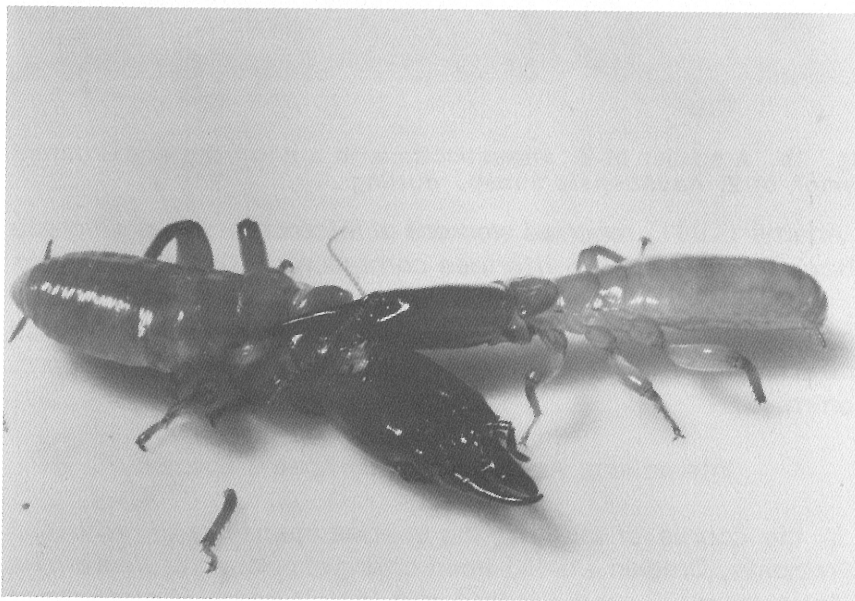


Fig. 1a. Soldiers of *Zootermopsis nevadensis* subsp. *nuttingi* and *Z. angusticollis* in combat. The *Z. nevadensis* soldier (right) has successfully defeated the *Z. angusticollis* soldier; legs have been severed and the head of the *Z. angusticollis* soldier has nearly been cleaved from its body.

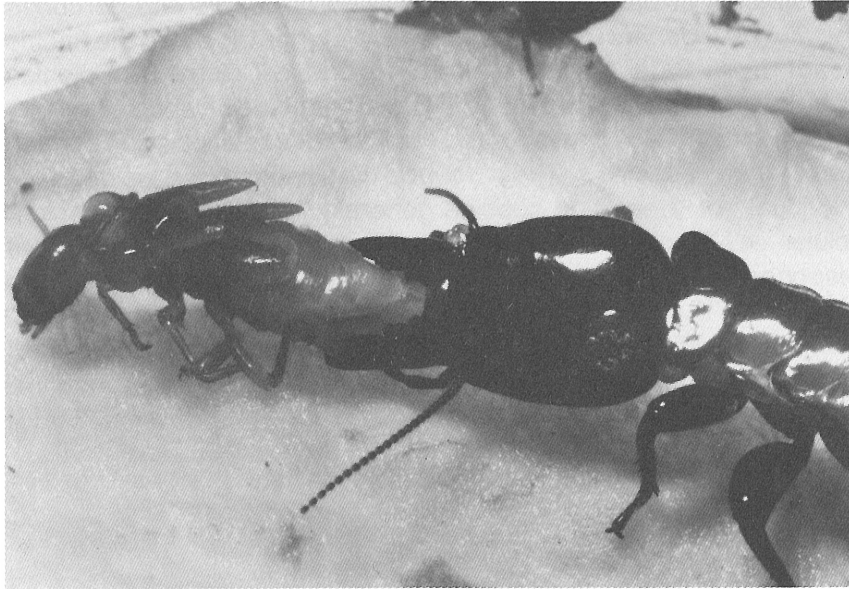


Fig. 1b. A soldier of *Z. angusticollis* with a captured and crushed nymph of *Z. nevadensis* subsp. *nuttingi*.

Adams (1991) reported workers of *Microcerotermes arboreus* attack workers of *Nasutitermes corniger* more than conspecifics from other nests. He also found that this reaction is innate; intense agonism toward *Nasutitermes* was shown by naive workers reared in the laboratory from founding reproductives (E.S. Adams, pers. comm.).

Interactions Among Other Sympatric Species

In the course of studying the species specificity of protozoan symbionts, Dropkin (1946) used chilling of colonies of *Neotermes* (*Kalotermes*) *jouteli* (Banks) and *Incisitermes* (*Kalotermes*) *schwarzi* (Banks) to facilitate mixing with congeners, even colonies of other families of termites. The chilling treatment made it possible to avoid the typical reaction of these two species, "violent, mutual attack," to termites of the other species. By eliminating the initial agonistic behavior, Dropkin demonstrated that *K. schwarzi* can be "infected" with protozoa from *N. jouteli*

and hypothesizes that the agonistic behavior of the termites is responsible for isolation of the protozoan fauna of these two species of termites.

Interactions Among Allopatric Species

Agonistic behavior has been demonstrated between termite species or subspecies that are not sympatric in their distributions. This illustrates that at least some termite species are able to discriminate other termites with which they have had no experience in recent history. It also is apparent that this behavior is innate, not learned or acquired.

Traniello and Beshers (1985) challenged laboratory colonies of *Nasutitermes costalis* with workers or soldiers from conspecific colonies, and from colonies of *N. corniger*, *N. nigriceps*, *N. ephratae*, *Microcerotermes* sp. and *Reticulitermes flavipes*. Of these species, the range of *N. costalis* does not overlap with *N. corniger*, *Microcerotermes* sp. or *R. flavipes*. The investigators measured the tendency of the "host" colony to recruit soldiers to defend the colony. There was virtually no recruitment to challenge *Microcerotermes* sp. or *R. flavipes*. Rather, their reaction was to retreat back to the colony and tighten the defensive line of soldiers, a response similar to mechanical prodding or to an ant. They found that the reaction of the host colony was greatest toward conspecifics and *N. corniger*, and less dramatic toward *N. nigriceps* and *N. ephratae*. The strong agonistic response of *N. costalis* to *N. corniger* may reflect the close phyletic relationship of these two species, which are virtually morphologically indistinguishable and have very similar cuticular hydrocarbon patterns (Howard *et al.* 1988, Haverty *et al.* 1990).

Examining interactions between and within species of the damp-wood termites, *Zootermopsis*, Haverty and Thorne (1989) reported that agonistic behavior occurred commonly among allopatric species. Colonies of *Z. laticeps* (Banks), which are geographically isolated from and ecologically dissimilar to the other species in this genus, reacted aggressively to all of the other species of *Zootermopsis*. In the species complex *Z. nevadensis* (Hagen) passive reactions are observed among conspecifics, but aggression is common in interactions with a closely related (morphologically indistinguishable) species or subspecies. Aggressive

behavior was dramatic between the sympatric species *Z. angusticollis* and *Z. nevadensis* subsp. *nuttingi*, but not between the allopatric species, *Z. angusticollis* and *Z. nevadensis* subsp. *nevadensis*. This behavioral discrimination and distinct hydrocarbon patterns justified a taxonomic division of *Z. nevadensis* (Haverty *et al.* 1988, Haverty and Thorne 1989).

AGONISM USED AS A BIOASSAY TO DETERMINE FORAGING AREAS

If a species under study consistently expresses some sort of distinctive recognition behavior during intraspecific encounters, elicitation of that response as a bioassay can be used to delimit the foraging territory of individual colonies. Termites are collected from spatially distributed forage or baits in the field, then assayed to determine colony affinity. Increased sampling density, particularly at suspected boundaries of territories, results in a higher resolution map of the foraging area. Bioassays can be a useful tool since termite foraging routes are often diffuse and irregularly dispersed from the central nest (even position of the "nest" is generally unknown in subterranean species). Tracking individual foraging tunnels is highly impractical in most environments, although it has been done in great detail for a few individual colonies (King and Spink 1969, Darlington 1982, Greaves 1962).

Nel (1968) used field bioassays of workers to define the foraging areas of *Hodotermes mossambicus* in pastoral regions of South Africa. Haverty *et al.* (1975) recognized that colony territories (loosely determined by monitoring attendance within a grid of toilet paper rolls) of the desert termite *Heterotermes aureus* did not appear to overlap, and that "neutral zones" occur between most of them. These researchers postulated that discrete boundaries may be maintained by intraspecific aggression, behaviors which were later confirmed by Binder (1988) and used by Jones (1990), in conjunction with marking and recapturing foragers, to map territories of *H. aureus*. S.C. Jones (unpubl. obs.) has directly observed fighting once among *H. aureus* colonies in the field; dead bodies were found on another occasion at the same site.

The "cemetery pits" unearthed by Darlington (1982) during her excavation of *Macrotermes michaelseni* trail systems in Kenya

suggests that behavioral responses may enable investigators to track foraging systems in this species. Whether or not discriminatory behaviors can be elicited in an experimental test regime remains unknown, since Darlington observed that underground passages are poorly developed in areas of overlap between foraging areas of neighboring colonies.

Levings and Adams (1984) and Adams and Levings (1987) report a case in which aggressive responses were bioassayed to deduce foraging territory patterns within a community. *Nasutitermes corniger* and *N. nigriceps* foraging areas were mapped; data from agonistic bioassays and from tracking foraging tunnels concurred in defining colony territories. Intraspecific behavioral bioassays also enabled Pearce *et al.* (1990) to determine maximum foraging distances in three species of *Microtermes* in Sudan. They conclude that considerable spatial colony overlap seems to occur in this ecosystem, and that interspecific aggression may also occur in the field.

VARIATION IN AGONISTIC RESPONSES

Throughout the literature on termite-termite encounters, reference to variation in behavioral response, even under consistent experimental conditions, is common. Intensity and outcome of these agonistic encounters seems to depend on the species, colonies and castes involved.

Andrews (1911) reported a test of two colonies of *Nasutitermes nigriceps* (or perhaps *N. costalis*) in Jamaica, collected a quarter of a mile apart, in which one showed mild hostility to the other, and the second reacted passively to the first. He then tested these two colonies against seven others, and observed a spectrum of responses from "peace" to "vicious attack," depending on the colonies involved. Andrews concluded that response varies with nest of origin and also with the particular individuals involved in the encounter.

Thorne (1982a) made similar observations between conspecifics of both *N. corniger* and *N. ephratae* in Panama. Even in these species, which typically show high aggression in intraspecific encounters, meetings between individuals from some (rare) geographically separated nest pairs show no overt aggressive behaviors. Anagonism was also observed within Panamanian

Nasutitermes, among individuals collected from widely separated nests, by Levings and Adams (1984) and Adams and Levings (1987). Variable levels of aggression among colonies have also been reported in *Reticulitermes* (Clément 1978, 1982, 1986), *Coptotermes acinaciformis* (Howick and Creffield 1980), *C. formosanus* (Su and Scheffrahn 1988, Su and Haverty 1991), *Amitermes beaumonti*, *Armitermes chagresi* (Thorne 1982a), *Zootermopsis angusticollis*, *Z. nevadensis* subsp. *nevadensis*, *Z. nevadensis* subsp. *nuttingi* (Haverty and Thorne 1989) and *Heterotermes aureus* (Jones 1990).

Data from Ikehara (1966) also show variation in response in a variety of termites from the Ryukyu archipelago, but it is unclear whether the groups tested in his experiments are from the same or different colonies. Both Ikehara (1966) and Thorne (1982a) note that interactions between some species show trends of dominance (a consistent or predictable 'winner' emerges); other pairings are unpredictable and depend on colony or individuals involved (variable from trial to trial). Su and Haverty (1991) have shown that some colonies of *Coptotermes formosanus* are consistently dominant or submissive to others.

Exogenous and endogenous factors can affect aggressive behavior. Clément (1986) observed a seasonal pattern in agonism of european *Reticulitermes*. In wet or oceanic climates, societies were open in the summer; in winter and under dry, semiarid conditions, colonies were closed (see INTRASPECIFIC INTERACTION section). Springhetti (1986) found the aggressiveness of pseudergates of *Kalotermes flavicollis* to be somehow stimulated by the presence of the royal pair. In studies of *Zootermopsis*, Haverty and Thorne (1989) reported that soldier-soldier encounters yielded the most consistent responses; pseudergate-pseudergate and soldier-nymph behaviors showed less consistent patterns.

It is not surprising that agonistic responses in termite interactions vary with species, population, colony, castes and even individuals involved. Especially given the highly artificial regime of most experimental protocols, lack of natural context and presence of exogenous stimuli will predictably interfere with results. Further, it is reasonable to assume that aggressive response depends on a suite of historical factors in each population and colony, perhaps to the level of individuals. Such variables as genetic relatedness,

colony size and health, reproductive status, density, nutrient availability and individual life histories likely influence expression of agonism. If a significant component of termite recognition cues are based on some sort of colony-specific chemical signature, it is possible that pattern combinations may be occasionally duplicated within a species, and thus account for rare cases of docile encounters between select colonies in a typically aggressive species.

COMPONENTS OF RECOGNITION/DISCRIMINATION CUES

The social, chemical and/or environmental stimuli which termites use to discriminate colony-mates from non-colony-mates are unknown, but have been the topic of considerable suggestion and postulation. Dudley and Beaumont (1889) first suggested "odor" as the recognition cue. Emerson (1929) mentioned that individuals from two *Nasutitermes banksi* Emerson colonies were "induced" to join by mixing the termites in a jar along with nest particles and infested wood from each colony. He suspected that the colony odor of each group "had been mixed through the forced association, and the individuals had learned to recognize the resultant odor as the right one to stimulate cooperation." Odor is also endorsed by Ribbands (1965). Stuart (1970) proposed colony-specific recognition pheromones.

Tactile contact with antennae or palpi has been an observed precursor to agonistic behavior (Stuart 1970; Clément 1982, 1986; Binder 1988; Haverty and Thorne 1989), and has led to speculation that components of the cuticle are perceived by contact (chemoreception by antennae or palpi) and that their variations launch aggression (Clément 1982, 1986). It is now established that surface hydrocarbons of termites and many other insects frequently show species-specific patterns (Howard and Blomquist 1982, Howard *et al.* 1982). Hydrocarbons may be involved in recognition (Howard *et al.* 1980, 1982, Clément 1986, Clément *et al.* 1988, Haverty and Thorne 1989, Bagnères *et al.* 1990, Su and Haverty 1991), but hydrocarbon components or profiles do not consistently predict agonistic response (Haverty and Thorne 1989, Bagnères *et al.* 1990, Su and Haverty 1991).

Studies on diet have been limited, but a change in host wood does not appear to be correlated with recognition in Clément's

(1986) study of *Reticulitermes*. Sands and Lamb (1975) however, cite evidence of larval immunity to attack [reported by Dudley and Beaumont (1889) and Andrews (1911)] as an indication that colony odor may have a dietary as well as a genetic component. They contend (p.193), "The simplest explanation of the immunity of the very young alien larvae to attack would be that, since they had been fed exclusively on stomodeal salivary food, they did not acquire the odour of their original colony so rapidly as the older forms that get stomodeal solids." In light of recent findings, an alternative explanation for larval immunity is that these juvenile cuticles are unsclerotized and therefore have surface chemistry which differs from that of mature colony mates.

Evidence of altered recognition or response cues may provide some insight into the mechanism of natural components. Certain treatments have been shown to interfere with recognition or aggressive behaviors. Dudley and Beaumont (1889) reported that *Nasutitermes* individuals washed for a few minutes in water, dried and then returned to their own colony are attacked (observations repeated and confirmed by Andrews (1911) in Jamaica). Andrews (1911) notes that washing insects in rain water renders them "neutral," but acknowledges that washes may also alter expression of normal behaviors. Andrews also experimented with washing workers in an "alien extract," brewed by leaving insects in water until they were "whitish." Workers emerging from the alien treatment were accepted by the alien colony. Both Dropkin (1946) and Howick and Creffield (1980) noticed reduced aggression in termites subjected to chilling. Howick and Creffield (1980), however, saw no effect of nest material in their study of *Coptotermes acinaciformis*.

Recognition and discrimination processes may involve a complex set of stimuli and behaviors, and different mechanisms may be identified among species. Su and Haverty (1991) hypothesize that different stimuli may act as releasers of agonistic behavior within a species, depending on context. Adams (1991) demonstrated that *Microcerotermes arboreus* distinguishes nestmates from other conspecifics on the basis of odor. Through controlled breeding experiments, he was able to determine that there is a genetic component to this nestmate recognition. Workers of *M. arboreus* were less aggressive toward unfamiliar relatives than toward familiar relatives. However, the unfamiliar relatives were

attacked more often than nestmates, despite their similar genetic composition. Adams concluded that "nestmate recognition is not based solely upon heritable characteristics of individual workers;" his results are consistent with the multiple stimulus hypothesis of Su and Haverty (1991).

POTENTIAL USES OF AGONISTIC BEHAVIORS IN TERMITE CONTROL

Natural aggressive behaviors between termite colonies might be used constructively either in bioassays to learn more about the biology of a particular species, or directly in termite control. In species showing consistent intraspecific aggression, agonistic behaviors could be used to precisely map the foraging territory of a given colony (Nel 1968, Levings and Adams 1984, Adams and Levings 1987, Pearce *et al.* 1990, and Jones 1990), or to track the fluidity of foraging ranges over time.

Knowledge of termite colony foraging areas would be useful in studies of colony population size, growth rate, and the density of colonies within a community. In treatment procedures, definition of colony foraging areas may become crucial as control techniques using bait toxicants are developed. Current data suggest that use of agonistic bioassays in mapping colony foraging areas will not work reliably in United States populations of *Coptotermes formosanus* because intraspecific mixtures of these termites are either unpredictable (Hawaii) or docile (Florida) (Su and Scheffrahn 1988, Su and Haverty 1991). Little is known about patterns of agonism in *Reticulitermes*, the other dominant subterranean pest in the U.S.

Perhaps the most promising and intriguing outcome of the study of termite agonistic behaviors is that such work might ultimately lead to an understanding of the recognition code(s) used by termites to discriminate colony mates from non-colony mates. Once the discrimination process is understood, applied approaches could be designed around the theme of masking or interfering with recognition stimuli. Manipulation of recognition and response cues could be used to enable chemically loaded intruders to enter a colony, to potentially instigate a civil war, to impregnate building materials with an offensive behavioral stimulus to prevent termite colonization, or to mask the presence of a toxicant to increase the ingestion of toxic baits.

Very generally, any stimulus that aggravates termites is potentially useful in termite control. The scientific goal is to find a stimulus that repels termites, or triggers an avoidance response. However, this stimulus must cause a persistent avoidance or repulsion, with little or no habituation. If the termites acclimate to the stimulus, it will no longer elicit the desired response. Control applications involving behavioral bioassays or live termites as an integral part of the pest management program will require trained operators and, typically, a longer treatment period than with chemical applications. Expense is predicted to be higher because of the labor involved in culturing and sampling termites. Integrated approaches may be beneficial in a variety of circumstances. However, in cases where little or no pesticides are desired in the infested area, control methodologies which make use of natural behavioral repertoires may provide effective alternatives.

CONCLUSIONS

Agonistic behavior among termites was first observed and reported in the nineteenth century. The majority of the research into this phenomenon has been descriptions of the overt fighting, fleeing, defensive or avoidance behavior. This review attempts to compile and summarize the disjointed approaches and interpretations made to date regarding agonistic behavior among Isoptera. It is clear that future research efforts are needed to substantiate, refine and broaden these results and conclusions.

Many behaviors between termites of different colonies may be more subtle than overt aggression, avoidance, or apparent tolerance. Fine scale ethological studies of intercolony interactions must be done to investigate the spectrum between fighting and "passive" responses, and to isolate the stimuli evoking each category of response. The neurobiology of chemoreception has never been examined in termites, but this approach should be tractable and could help, for example, in our understanding of the possible role of cuticular hydrocarbons (or fractions of these lipids) in termite-termite recognition processes. A detailed understanding of agonistic behavior among termites could help us identify natural, biologically active compounds with potential for practical applications, and would perhaps reduce our reliance on large quantities of termiticides and wood preservatives to protect wood in use.

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