An Assessment of the Potential Uses of Agonistic Behaviors in Termite Control[1]

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Abstract: The potential use of termite-termite agonism in pest control is explored and evaluated. Intra- and interspecific encounters among termites from different colonies are known to result in aggressive or avoidance behaviors in a variety of species. Recent studies suggest, however, that intraspecific confrontations only rarely evoke aggressive responses in several economically important termite genera in the United States (Coptotermes, Reticulitermes, and Zootermopsis). Thus the most promising applied use of natural agonistic behaviors among termites appears to be in research on individual- and colony-recognition systems in the Isoptera. Artificial manipulation of recognition and response cues might facilitate novel control methodologies based on masking or interfering with natural stimuli. Directions for future research are discussed.

Insect behaviors are diverse, and knowledge of the behaviors of a species has always been a key element in pest management. Basic knowledge of activity periods, diet preferences, and mating behaviors can be central in determining an approach toward deterring a pest species. Taking advantage of behavioral patterns or interfering with natural repertoires or both can produce very effective control methodologies.

Understanding the foraging behavior of subterranean termites is crucial to prevention of damage to buildings (Beal and others 1989; Su and Scheffrahn 1990). Preventative techniques include proper construction practices to exclude or deter foraging and feeding by subterranean termites and application of large volumes of chemical insecticides as soil drenches to kill or repel foraging subterranean termites. Existing and future methods for remedial control of subterranean termites will also rely on knowledge of the foraging behavior of these insects (Su and Scheffrahn 1990).

Two promising future control methods involve the use of physical barriers and the use of nonrepellent, slow-acting insecticides. Physical barriers will consist of a substrate that has a particle size impenetrable to subterranean termites (Su and Scheffrahn 1990). Nonrepellent, slow-acting insecticides will be used in baits or in baiting systems. Subterranean termites will recruit to the bait stations through natural foraging behaviors and feed on the chemically impregnated wood. It is then hoped that they will return to their colony and feed their insecticide-laced crop contents to colony mates before dying. Normal foraging behaviors will thus cause an entire colony to be slowly poisoned by toxic baits. Termite colony populations will become depressed, and they will ultimately be eliminated, not simply excluded, from structures.

Another behavior that has recently received attention by termite biologists is agonistic behavior. Agonistic behavior involves social interactions between individuals, including submitting, fleeing and fighting, even to death. Termites show a wide range of agonistic behaviors when interacting with termites from a different colony. In all cases studied to date, termites from colonies of different sympatric species respond aggressively when they meet (Adams and Levings 1987; Clément 1982; Grassi and Sandias 1896-1897; Haverty and Thorne 1989; Nel 1968; Springhetti and Amorelli 1982; Thorne 1982; Traniello and Beshers 1985). Intraspecific confrontations also result in clear aggressive or avoidance behaviors in a variety of termite species (Adams and Levings 1987; Andrews 1911; Binder 1988; Clément 1986; Dudley and Beaumont 1889; Howick and Creffield 1980; Jones 1987; Levings and Adams 1984; Nel 1968; Pearce and others 1990; Pickens 1934; Su and Haverty 1991; Thorne 1982). Since many of these termite-termite interactions result in injury or death to some or all of the insects, it is reasonable to evaluate their potential use in control of termites as structural pests.

CASE STUDY: THE DAMPWOOD TERMITE GENUS Zootermopsis

From an individual termite's viewpoint, the fundamental problem in encounters with other termites is the correct discrimination of colony mates from noncolony mates. We examined intra- and interspecific interactions among all species of Zootermopsis Emerson in the Pacific coastal states and southwest deserts of the United States (Haverty and Thorne 1989). Those results are summarized here, and new data on response of naive soldiers from incipient colonies are reported.

Zootermopsis laticeps (Banks) is morphologically distinct from other members of the genus. This species also has an isolated geographic range in Arizona, New Mexico, and northern Mexico, and lives in dead portions of live trees, usually in riparian situations. In the absence of alates, the morphological characters used to differentiate the described species Z. angusticollis (Hagen) and Z. nevadensis (Hagen) were ambiguous. That imprecision made it impossible to establish valid experimental encounters between colonies. This problem was resolved when Haverty and others (1988) discovered three consistent and distinct cuticular hydrocarbon phenotypes among the two "species," Z. angusticollis and Z. nevadensis, that occur

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along the Pacific Coast. The hydrocarbon separations enabled us to isolate a diagnostic character, shape and position of the subsidiary tooth on the right mandible of nonsoldiers, which established unambiguous discrimination of Z. angusticollis from Z. nevadensis (Thorne and Haverty 1989).

Z. angusticollis shows one distinct hydrocarbon profile throughout its range (labelled phenotype II by Haverty and others [1988]). Two hydrocarbon phenotypes (I and III) are associated with the single morphological species Z. nevadensis, but each chemical phenotype has a discrete geographic distribution and may have temporal isolation in alate phenologies (Haverty and others 1988; Haverty and Thorne 1989; Thorne and Haverty 1989; Weesner 1970). In our experiments we investigated whether intra- or inter-hydrocarbon phenotypes of Zootermopsis colonies show discrimination in behavioral encounters.

In the laboratory we set up pairwise experimental trials in which we placed combinations of various castes from different hydrocarbon phenotypes into petri dish arenas lined with filter paper. Responses were recorded on a ranking system from no noticeable reaction to immediate lethal attack. Observed behaviors were typically either docile or highly aggressive, with little intermediate response.

General results of these experiments are summarized here (for more detail see Haverty and Thorne 1989). In intraphenotype pairings, agonistic reactions among members of any castes are rare, except between some colonies of Z. angusticollis. Interphenotype interactions frequently stimulate aggressive responses (fig. 1), but behaviors vary depending on which colonies are involved. Z. angusticollis and Z. nevadensis phenotype III, which occur sympatrically throughout much of their range, are more aggressive towards each other than are Z. angusticollis and Z. nevadensis phenotype I, which have an allopatric distribution. The two hydrocarbon phenotypes of Z. nevadensis do show discrimination responses in behavioral encounters, and in that way act like distinct species. The behavioral discrimination was further evidence to justify designation of the Z. nevadensis complex into two subspecies, Z. nevadensis subsp. nevadensis (Hagen) [phenotype I] and Z. nevadensis subsp. nuttingi (Haverty and Thorne) [phenotype III] (Haverty and Thorne 1989).

Supplementing experiments reported in Haverty and Thorne (1989), we have recently conducted a series of comparable trials involving young, naive soldiers from experimentally bred laboratory colonies. In July and August 1987, the wings of mature male and female Z. nevadensis subsp. nuttingi alates from a variety of colonies were removed and the alates were paired in small petri dishes lined with moist sand and containing a piece of Douglas-fir wood. Many of these couples successfully reared offspring. The first soldier differentiated when brood size reached approximately 15-20 individuals. In March 1989 we removed these young soldiers from incipient colonies which still contained both primary reproductives, and introduced each soldier to three nymphs or larvae from a haphazardly selected colony of Z. nevadensis subsp. nevadensis [14 trials] or Z. angusticollis

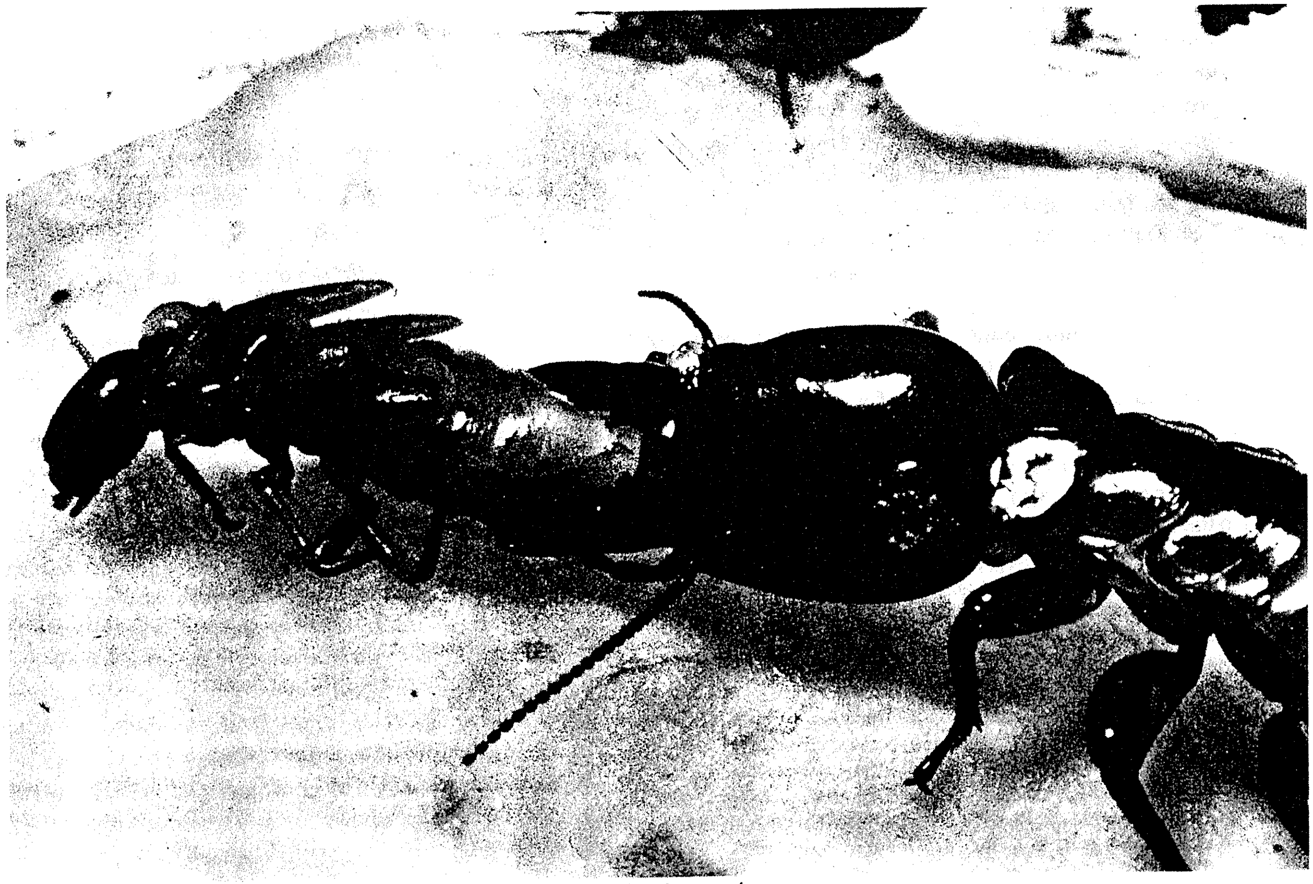
Figure 1—Zootermopsis angusticollis soldier attacking a Z. nevadensis nymph.

[10 trials]. Each soldier was used only once (experimental protocol identical to that described for Haverty and Thorne 1989, Experiment 1). In the Z. nevadensis subsp. nuttingi versus Z. nevadensis subsp. nevadensis encounters, naive Z. n. subsp. nuttingi soldiers attacked and killed Z. n. subsp. nevadensis larvae or nymphs in 5 of the 14 trials. In all 14 cases soldiers showed agonistic responses by repeatedly flaring their mandibles. Results of the Z. nevadensis subsp. nuttingi soldier encounters with Z. angusticollis larvae or nymphs were consistent: in each of the 10 cases the soldiers attacked and killed the Z. angusticollis. These data on naive soldiers parallel results from the experiments using soldiers from mature field colonies reported in Haverty and Thorne (1989).

The generally docile reactions observed in the intraphenotype trials raised the possibility that passive fusion might occur between members of two conspecific field colonies whose gallery networks met in a host log. We have demonstrated experimentally, however, that soldiers, nymphs, and pseudergates will kill and consume functional reproductives from a foreign colony, even within the same hydrocarbon phenotype. Thus, complete colony fusion in nature is unlikely (Haverty and Thorne 1989). Aside from Zootermopsis, the only cases of passive coalescence of termite colonies reported in the literature involve Reticulitermes (Rhinotermitidae) (Clément 1986; Jones 1987) and some populations of Coptotermes (Rhinotermitidae) (Su and Haverty 1991; Su and Scheffrahn 1988).

The stimuli responsible for aggressive behaviors in Zootermopsis or other species of North American termites are unknown. Clearly, however, the rapidity, consistency, and efficiency of these aggressive responses are effective in termite-termite interactions. In the remainder of this paper we examine realistic potential uses of these natural behaviors as elements of pest management strategies.

POTENTIAL APPLIED USES OF TERMITE AGONISTIC BEHAVIORS

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. As an example, in species showing consistent intraspecific aggression, agonistic behaviors could be used to precisely map the foraging territory of a given colony (technique used by Pearce and others 1990). Termites from different locations could be observed in encounters with (A) individuals known to be from the focal colony and (B) members of a geographically distinct, conspecific colony. A passive response to sample A and an aggressive response to B would suggest that termites in the test sample were foragers from the same colony represented in sample A (but responses of termites to neighbors versus strangers has not yet been studied [see Gordon 1989]). An agonistic response to both groups A and B would mean that the termites in the test sample were from a separate (third) colony.

Precise knowledge of the foraging areas of a termite colony would be useful in studies of colony population size, growth rate, foraging range, and the density of colonies within a community. In treatment procedures, knowledge of foraging areas may become crucial as control techniques using bait toxicants are developed. Unfortunately, use of agonistic bioassays in mapping colony foraging areas will not work reliably on any of the two dominant genera of subterranean termite pests in the United States (Reticulitermes and Coptotermes), because intraspecific mixtures of these termites are generally docile. (Broad variability in degree of agonistic response among termites from different colonies or populations or both has been noted by Haverty and Thorne 1989; Su and Haverty 1991; Su and Scheffrahn 1988; Thorne 1982.)

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 noncolony mates. Recognition may involve cuticular hydrocarbon components (Howard and Blomquist 1982; Howard and others 1980, 1982); other behavioral and chemical cues are likely involved as well. Once the discrimination process is understood, numerous 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, or to impregnate building materials with an offensive, behavioral stimulus to prevent termite colonization.

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, but it must be a persistent avoidance or repulsion stimulus 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.

DIRECTIONS FOR FUTURE RESEARCH

Studies of Additional Taxa

Further studies on patterns of agonistic behavior within and among termite species will broaden our perspective on the potential uses of such aggressive or repulsive responses in termite control. Thus far, agonistic behaviors within and between Zootermopsis species have been studied (Haverty and Thorne 1989). Intraspecific agonism has been studied in Heterotermes aureus (Snyder) (Binder 1988; Jones 1987) and Coptotermes formosanus shiraki (Su and Haverty 1991). The genus Reticulitermes is the most economically important group of wood-destroying insects in the United States, yet little behavioral work has been done on the Reticulitermes species within the United States. This genus should definitely be the target of future research on intra- and interspecific agonistic behavior.

Chemoreception

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 role of cuticular hydrocarbons (or fractions of these lipids) in termite-termite recognition processes. Such studies would help us identify natural, biologically active compounds with potential for practical applications.

Detailed Ethological Analyses

Many of the 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 isolate the stimuli evoking each category of response.

Evaluation of Experimental Methodologies

Laboratory results should be confirmed in the field to validate the experimental protocols used to study dynamics between termite colonies. When intra- or interspecific encounters occur between termites in their natural social and physical environment, does one observe the same passive or aggressive reactions which are seen in laboratory trials involving small subsets of the same two colonies?

The methods for studying termite-termite encounters are still being devised and refined. Binder (1988) introduced some innovative approaches in his study of H. aureus. In one experiment he simulated a foraging arena with a balsawood barrier separating termites from separate colonies (dyed to differentiate colony affiliation). A high magnification video camera was used to document movements and behaviors over the 24 hours required for the termites to penetrate the barrier. Similar studies employing video equipment and image tracking software would expand our understanding of termite-termite behaviors. Eventually, standardization of protocols should be considered to facilitate comparisons between studies on related taxa.

REFERENCES

Adams, Eldridge S.; Levings, Sally C. 1987. Territory size and population limits in mangrove termites. Journal of Animal Ecology 56: 1069-1081.

Andrews, E. A. 1911. Observations on termites in Jamaica. Journal of Animal Behavior 1: 193-228.

Beal, Raymond H.; Mauldin, Joe K.; Jones, Susan C. 1989. Subterranean termites—Their prevention and control in buildings. Home and Garden Bulletin 64. Washington, DC: U.S. Department of Agriculture, Forest Service, 36 p.

Binder, Bradley F. 1988. Intercolonial aggression in the subterranean termite Heterotermes aureus (Isoptera: Rhinotermitidae). Psyche 95(1-2): 123-137.

Clément, Jean-Luc. 1982. Signaux de contact responsables de l'agression interspécifique des Termites du genre Reticulitermes (Isoptera). Comptes Rendus des Séances de l'Académie des Sciences, Paris. 294: 635-638.

Clément, Jean-Luc. 1986. Open and closed societies in Reticulitermes (Isoptera, Rhinotermitidae): geographic and seasonal variations. Sociobiology 11: 311-323.

Dudley, Plimmon H.; Beaumont, Jean. 1889. Observations on the termites, or white-ants of the Isthmus of Panama. Transactions of the New York Academy of Science 8: 85-114.

Gordon, Deborah. 1989. Ants distinguish neighbors from strangers. Oecologia 81(2): 198-200.

Grassi, B.; Sandias, A. 1896-1897. The constitution and development of the society of termites: Observations on their habits, with appendices on the parasitic protozoa of Termitidae, and on the Embiidae. Quarterly Journal of Microscopical Science 39: 245-322; 40: 1-82.

Haverty, Michael I.; Page, Marion; Nelson, Lori J.; Blomquist, Gary J. 1988. Cuticular hydrocarbons of the dampwood termites, Zootermopsis: intra- and intercolony variation as potential taxonomic characters. Journal of Chemical Ecology 14: 1035-1058.

Haverty, Michael I.; Thorne, Barbara L. 1989. Agonistic behavior correlated with hydrocarbon phenotypes in dampwood termites, Zootermopsis (Isoptera: Termopsidae). Journal of Insect Behavior 2(4): 523-543.

Howard, Ralph W.; Blomquist, Gary J. 1982. Chemical ecology and biochemistry of insect hydrocarbons. Annual Review of Entomology 27: 149-172.

Howard, Ralph W.; McDaniel, C. A.; Blomquist, Gary J. 1980. Chemical mimicry as an integrating mechanism: Cuticular hydrocarbons of a termitophile and its host. Science 210: 431-433.

Howard, Ralph W.; McDaniel, C. A.; Nelson, Dennis R.; Blomquist, Gary J.; Gelbaum, Leslie T.; Zalkow, Leon H. 1982. Cuticular hydrocarbons of Reticulitermes virginicus (Banks) and their role as potential species- and caste-recognition cues. Journal of Chemical Ecology 8(9): 1227-1239.

Howick, C.D.; Creffield, J.W. 1980. Intraspecific antagonism in Coptotermes acinaciformis (Froggatt)(Isoptera: Rhinotermitidae). Bulletin of Entomological Research 70: 17-23.

Jones, Susan C. 1987. Foraging party and territory size of the desert subterranean termite Heterotermes aureus (Snyder) in a Sonoran desert grassland. Ph.D. thesis, University of Arizona, Tucson.

Levings, Sally C.; Adams, Eldridge S. 1984. Intra- and interspecific territoriality in Nasutitermes (Isoptera: Termitidae) in a Panamanian mangrove forest. Journal of Animal Ecology 53: 705-714.

Nel, J.J.C. 1968. Aggressive behavior of the harvester termites Hodotermes mossambicus (Hagen) and Trinervitermes trinervoides (Sjöstedt). Insectes Sociaux 15: 145-156.

Pearce, Michael J.; Cowie, Robert H.; Pack, Angela S.; Reavey, Duncan. 1990. Intra-specific aggression, colony identity and foraging distances in Sudanese Microtermes spp. (Isoptera: Termitidae: Macrotermitinae). Ecological Entomology 15(1): 71-77.

Pickens, A. L. 1934. The biology and economic significance of the western subterranean termite, Reticulitermes hesperus. In: Kofoid, Charles A., ed. Termites and termite control. Berkeley: University of California Press, 157-183.

Springhetti, Antonio; Amorelli, Maurizio. 1982. Competitive behavior between two species of Isoptera: Kalotermes flavicollis and Reticulitermes lucifugus. Sociobiology 7: 155-164.

Su, Nan-Yao; Haverty, Michael I. Agonistic behavior among colonies of the Formosan subterranean termite, Coptotermes formosanus Shiraki (Isoptera: Rhinotermitidae), from Florida and Hawaii: Lack of correlation with cuticular hydrocarbon composition. Journal of Insect Behavior 4(1): 115-128.

Su, Nan-Yao; Scheffrahn, Rudolf H. 1988. Intra- and interspecific competition of the Formosan and the eastern subterranean termite: Evidence from field observations (Isoptera: Rhinotermitidae). Sociobiology 14: 157-164.

Su, Nan-Yao; Scheffrahn, Rudolf H. 1990. Economically important termites in the United States and their control. Sociobiology 17(1): 77-94.

Thorne, Barbara L. 1982. Termite-termite interactions: Workers as an agonistic caste. Psyche 89: 133-150.

Thorne, Barbara L.; Haverty, Michael I. 1989. Accurate identification of Zootermopsis species (Isoptera: Termopsidae) based on a mandibular character of nonsoldier castes. Annals of the Entomological Society of America 82(3): 262-266.

Traniello, James F.A.; Beshers, Samuel. 1985. Species-specific alarm/recruitment responses in a Neotropical termite. Naturwissenschaften 72,S: 491-492.

Weesner, Frances M. 1970. Termites of the Nearctic Region. In: Krishna, K.; Weesner, F. M., eds. Biology of termites, Vol II. New York: Academic Press; 477-525.