

Review of Agonistic Behaviors in the Isoptera

by

Thomas G. Shelton¹ & J. Kenneth Grace¹

ABSTRACT

The cues involved in recognition of different individuals, different colonies, or different species by termites (Isoptera) are poorly understood. In the hope that a unified view of intracolony, intercolony, and interspecific recognition and agonistic behaviors may help to elucidate the general recognition mechanisms involved, this paper presents an overview of agonism in the Isoptera. Included are discussions of the levels of agonism observed among termites, defensive adaptations, and laboratory manipulation of agonism. Special emphasis is given to studies investigating intercolonial variability in the Formosan subterranean termite.

INTRODUCTION

While research focusing on termite control abounds, there are many areas of underlying termite biology that are poorly understood. For example, investigators have sought the cues that *Coptotermes formosanus* Shiraki uses for kin discrimination (Su & Haverty 1991). Thorne & Haverty (1991a & b) proposed that manipulation of the cues that termites use in kin recognition and that stimulate agonistic actions could be valuable in management of termite pests. However, laboratory studies with *C. formosanus* have demonstrated that intercolonial agonism does not always result from pairing colonies (Su & Haverty 1991, Shelton 1996), and that agonistic interactions do not appear to correlate with identifiable colony characteristics such as cuticular hydrocarbon patterns (Su & Haverty 1991). Investigations into other forms of intercolonial variation have found either no variation, as with mitochondrial DNA (Broughton & Grace 1994), or minimal variation, as with isozymes (Strong & Grace 1993). While a recent isozyme study demonstrated somewhat more variability among colonies (Wang & Grace 1995), no such characters have yet been correlated with agonistic behavioral patterns.

Recognition of kin and non-kin, aggressive responses to competitors (such as other termite species or even colonies within the same species), and defensive responses to predator such as ants can all be considered

¹Department of Entomology, University of Hawaii, 3050 Maile Way, Honolulu, HI, 96822-2271.

classes of agonistic behaviors. Despite their different motivations and outcomes, it seems likely that similar types of cues are involved in stimulating or suppressing these different behaviors. In the hope that a unified view of these behaviors may help to elucidate the general recognition mechanisms involved, this paper presents an overview of agonism as a whole in the Isoptera. Due to our own interest in the biology and behavior of *C. formosanus*, special reference is given to research investigating this species.

ALTRUISM AND AGGRESSION

Many behaviors exist in insect societies that do not appear to directly benefit the individual that performs them but instead may benefit the society as a whole, at some personal fitness cost to that individual (Wilson 1975). Altruism is defined as an act that has a direct personal fitness cost for the acting individual, while benefitting an individual that is a relation, or no relation at all (Wilson 1975). Altruistic behaviors have previously been considered to include feeding behaviors (trophallaxis and proctodeal feeding) and aggression in colony defense (Wheeler 1928). However, suggestions made more recently regarding feeding behaviors in the Isoptera have indicated that these behaviors may not have a significant fitness cost for the donor and should therefore not be considered truly altruistic functions (Myles & Nutting 1988). The ultimate altruistic act for a social insect is to die in defense of its colony (Myles & Nutting 1988).

It would appear important for social insect species to evolve discrete and specific mechanisms for nestmate or kin discrimination, especially for subterranean species that are likely to encounter foragers of other colonies. Lacking a discrete discrimination system could leave a colony vulnerable to social parasitism by nest invaders of all types (Wallis 1964).

In eusocial species, altruistic behavior occurs within single colonies, and nestmates within these colonies are capable of distinguishing themselves from non-nestmate conspecifics (Wallis 1964). This limitation to intracolony behavior is not always exhibited (Clement 1986, Su & Scheffrahn 1988a), and can be modified under experimental conditions (Andrews 1911; Dropkin 1946; Howick & Creffield 1980; Springhetti & Sapigni 1984, 1990). Grace (1996) found no evidence of agonism among *Reticulitermes flavipes* (Kollar) colonies in Ontario, Canada, possibly because of high relatedness resulting from a very limited number of termite introductions to the region and frequent "budding" of new colonies from old. Clement (1986) viewed termite colonies as either being 'open' or 'closed', depending upon their reaction to non-

nestmates. Some colonies may be plastic, *i.e.*, they are 'open' at certain times of the year, and 'closed' at other times, and Clement (1986) reported that the variability between open and closed colonies in the *Reticulitermes lucifugus* (Rossi) complex varied with the environment of the colony. Lai's (1977) examination of Hawaiian colonies of *C. formosanus* suggested that they were typically closed. In many cases, discrimination of non-nestmate conspecifics results in agonistic behavior between individuals (Andrews 1911, Wallis 1964, Nel 1968, Thorne 1982, Binder 1988, Su & Scheffrahn 1988a, Delaplane 1991, Su & Haverty 1991, Thorne & Haverty 1991a).

Aggression in eusocial insects.

Identifying the cues involved in the kin discrimination process for a social insect species is an important step in understanding the communication abilities of these insects. The expected result of interactions between a social insect and an alien is aggression (Wallis 1964, Levings & Adams 1984, Thorne & Haverty 1991a). One key to discovering kin recognition cues is the examination of agonism in the social insect species as it occurs under natural conditions, either intraspecifically or interspecifically. Agonism between colonies of conspecifics or different species may also be manipulated in the laboratory, providing information on communication. Wallis (1964) summarized the four functions of aggressive behavior in the social insects: 1) colony cohesion; 2) intraspecific competition, a point emphasized by the use of agonism to delineate colony foraging areas in the Rhinotermitid *Heterotermes aureus* (Snyder) (Jones 1990, 1993); 3) interspecific competition, whether for foraging material or territory; and 4) hunting behavior in predatory social insects, such as wasps and ants.

Adams (1991) mentioned similar themes for the evolution of aggression along with sociality in insects. He stated that the kin selection theory of the evolution of sociality depends on animals exhibiting direct altruistic behavior toward their close genetic relations (see also Wallis 1964; Wilson 1971, 1975; Myles & Nutting 1988). This reasoning was the basis for a study on the heritability of colony recognition cues in *Microcerotermes arboreus* Emerson. If insects use heritable cues to distinguish between relatives and non-relatives, this provides a mechanism for altruism among only those insects that are closely related (Adams 1991). He also stated that it is easier to achieve such a mechanism in haplodiploid animals (*e.g.*, ants) than in diploid animals (*e.g.*, termites). However Adams' (1991) experimental data demonstrated that in *M. arboreus*, colony recognition cues were capable of being passed from one generation to the next through either parent.

Su and Scheffrahn (1988a) suggested that *C. formosanus* aggressive behavior was exhibited only interspecifically during early introduction stages. This allowed for less competition between conspecifics, thereby increasing the chances for establishment of the species. The authors observed that early introductions of *C. formosanus* in Florida resulted in open colonies which did not exhibit intercolonial aggression, suggesting the possibility of colony fusion. This was in contrast to Hawaiian populations which were more closed and therefore exhibited intercolonial agonism (Lai 1977, Su & Haverty 1991). The authors suggested that this was the result of the Hawaiian populations being much longer established (Su & Scheffrahn 1988a). Other researchers have used intercolonial aggression among conspecifics to examine foraging territory sizes in the Rhinotermitidae (Jones 1990, 1993) and the Termitidae (Pearce *et al.* 1990).

DEFENSIVE ADAPTATIONS

Survival to any animal means the acquisition of resources, food and/or territory, on both large and small scales (Price 1984). Animals use two means of retaining acquired resources, exploitation and defense (Krebs & Davies 1993). Resource defense, either by aggressive display or actual combat, allows animals to prevent competitors, both conspecific and other species, from exploiting those resources (Krebs & Davies 1993). Social insects must defend their resources on a constant basis (Wilson 1971, Krebs & Davies 1993).

In the Isoptera, defenses against predation are an absolute necessity that must be vigilantly upheld, otherwise the colony will be overrun by an invasive enemy (Wallis 1964). This type of predation is associated with the big-headed ant, *Pheidole megacephala* (Fabricius) which often nests in wood occupied or vacated by the Formosan subterranean termite in Hawaii (Cornelius & Grace 1995). In addition to preying on *C. formosanus*, *P. megacephala* competes spatially for nesting sites (Cornelius & Grace 1995). Worker populations of some termite species can number in the millions of individuals in single colonies (Su & Scheffrahn 1988b, Grace *et al.* 1989, Grace 1992, Su *et al.* 1993). Haverty (1977) listed the soldier composition of various termite species. *C. formosanus* can have over a million workers in a single colony (Su & Scheffrahn 1988b) with soldiers constituting about 10% of its colony (Haverty 1977). Haverty (1979) as well as Su and LaFage (1987a) have suggested that the optimal soldier proportions for *C. formosanus* may be as high as 25% of the foraging population. Although workers are capable of exhibiting agonistic behavior (Andrews 1911, Thorne 1982, Thorne & Haverty 1991a), the soldier caste has evolved to defend the

colony (Wheeler 1928, Kofoid 1934), and is so modified for this role that it is unable to feed and must be provided food by trophallaxis from workers (Su & LaFage 1987b).

Chemical defenses.

As a group, termites have developed extraordinary methods of defense, particularly those of a chemical nature (Blum *et al.* 1982; Scheffrahn *et al.* 1983, 1987, 1988; Prestwich 1984; Clement *et al.* 1988; Prestwich 1988; Bagnères *et al.* 1990; Chuah *et al.* 1990; Goh *et al.* 1990; LeMaire *et al.* 1990; Roisin *et al.* 1990; Valterova *et al.* 1993). Three glands are primarily involved in the chemical defenses of the Isoptera. These are the frontal gland in the Rhinotermitidae, Termitidae, and Nasutitermitinae (Quennedey & Deligne 1975, Roisin *et al.* 1990), the salivary gland in the Termitidae and Mastotermitidae (Prestwich 1984), and the cibarial gland in the Macrotermitinae (Prestwich 1984). These glands open on the head, and in some cases may have abdominal reservoirs (Prestwich 1984). Morphological changes occur with increasing dependence upon chemical as opposed to mechanical defense mechanisms (Prestwich 1984). Perhaps the most well known defensive alteration is seen in the Nasutitermitinae, where mandibles are vestigial, but soldiers possess an elongate rostrum that ejects either a monoterpene or a diterpene defensive secretion (Prestwich 1984, Levings & Adams 1984, Traniello & Beshers 1985). Other modifications include an elongate rostrum with piercing mandibles (*e.g.*, *Armitermes* spp.), and an elongate labrum modified to brush defensive secretions onto opponents (*e.g.*, *Acorhinotermes* spp.) (Prestwich 1984). Compounds used as defensive secretions are grouped into the terpenes (monoterpenes, sesquiterpenes, diterpenes), acetate-derived substances (quinones, alkanes, alkenes, nitroalkenes, vinyl ketones, ketoaldehydes, and macro cyclic lactones), and proteins and mucopolysaccharides (Blum *et al.* 1982, Prestwich 1984).

Mechanical defenses.

Diverse mechanical defenses are seen in various termite castes, most noticeably in the soldiers (Kofoid 1934, Zimmerman 1948, Prestwich 1984). Soldier mandibles may be enlarged and toothed for biting and crushing; elongate and slender for snapping or slashing; curved and pointed for piercing; or vestigial in order to place more emphasis on other cephalic modifications (Prestwich 1984). Other cephalic modifications include the familiar extended rostrum of the Nasutitermitinae, the enlarged phragmotic head of some Kalotermitids used to plug breaches in the colony's walls, and the labral brushes developed in the Rhinotermitidae (Kofoid 1934, Zimmerman 1948, Prestwich 1984).

Additional forms of mechanical defense are autothysis and abdominal dehiscence (Prestwich 1984). Autothysis is the result of forcing the contents of a labial gland reservoir through a weakened area of the abdomen or thorax, while abdominal dehiscence splits the abdominal wall due to vigorous defecation efforts while engaging in agonistic behavior (Prestwich 1984). Both methods result in 'exploding termites' or 'walking time bombs' of an entangling nature. These methods of abdominal rupturing can occur in both workers and soldiers (Prestwich 1984), and both may be seen as truly altruistic acts, since each results in the death of the acting individual (Wilson 1975, Myles & Nutting 1988).

AGONISM IN WORKERS

Although much information has been provided on the abilities of the soldiers to defend colonies, it should not be forgotten that workers also exhibit aggressive behavior (Andrews 1911, Thorne 1982, Thorne & Haverty 1991a). This is not surprising considering that colony workers far outnumber the soldiers and some termite species are known to be entirely soldierless (Haverty 1977, Prestwich 1984). While workers may be equipped with mechanical defenses such as autothysis or abdominal dehiscence the most common method of worker attack is mandibular biting of the abdomen or legs (Thorne 1982). However, direct attack is not the only method of dealing with alarm stimuli in termite workers. Working with two species of *Zootermopsis* (Termopsidae), Stuart (1967) found that a low level alarm in the nest resulted in nymph recruitment to the area, not for attack, but for reconstruction of sections of nest walls. He theorized that this behavior removes a stimulus of the alarm by exclusion rather than attack, suggesting that life in the colony returns to normal after the construction is complete. Stuart (1967) appended this by stating that high level alarm stimuli, such as an ant attack, are first handled by the soldiers, and that the resulting ant carcasses are considered low level alarm stimuli that promote building in the workers, thereby excluding any further chemical stimuli emitted by the ants. An important aspect of worker aggression is the activity of workers in agonistic behavior with regard to their soldier types and the type of opponent faced (Thorne 1982). The soldier complement of foraging *Nasutitermes* spp. is higher than that of mandibulate-soldiered species which forage in the open, suggesting that the *Nasutitermes* soldiers' defensive chemicals may be useful against non-isopteran opponents, but are not adequate to defend against other termites, for which workers are necessary (Thorne 1982).

Worker (or pseudergate) aggression also occurs in the Rhinotermitidae.

Binder (1988) noted that *Heterotermes aureus* (Snyder) workers would attack the head of a conspecific soldier from a different colony immediately, while soldiers presented with the head of a conspecific worker did not. He hypothesized that the soldier was unable to recognize the worker head as an alien because of immobility. He suggested that perhaps the vertical oscillatory movement (Howse 1965) action pattern often observed in alarmed termite workers may be necessary for soldier recognition in *H. aureus*. He also suggested that *H. aureus* soldiers may not involve themselves in intercolonial aggression similar to *Nasutitermes* spp. (Thorne 1982). *C. formosanus* also exhibits worker agonistic behavior in the absence of soldiers (Shelton 1996), as do the harvester termites *Trinervitermes trinervoides* (Sjostedt) (Termitidae) and *Hodotermes mossambicus* (Hagen) (Hodotermitidae) (Nel 1968).

AGONISM IN REPRODUCTIVES

Reproductive termites are also capable of exhibiting agonistic behavior, although there is little information available and some is anecdotal (Emerson 1933, Nel 1968, Myles & Chang 1984, Myles 1988). In a *Reticulitermes arenicola* Goellner lab colony, Emerson (1933) observed two of three mature queens fighting while none of the other termites (including the third queen) showed any indication of being alarmed. The defeated queen was quickly cannibalized by the workers after the fight ended (Emerson 1933). Interestingly, he noted that the victorious queen sustained a leg injury which did not induce cannibalism among the workers in the manner of the defeated queen.

Myles and Chang (1984) gave evidence for similar agonistic behavior in replacement reproductives of *Neotermes connexus* Snyder (Kalotermitidae). When nymphs molted into replacement reproductives, which fought among themselves, only one replacement reproductive remained uninjured. In studies using only the replacement reproductives, the losing termites were not cannibalized as when such bouts take place in the presence of nymphs. This indicated that the cannibalistic behavior of the nymphs was merely a clean-up activity. In studies including soldiers, nymphs, and replacement reproductives, only the replacement reproductives take part in these battles, which begin in a rather ritualized manner. Individual replacement reproductives investigate one another using their palpi to examine the other in an anterior to posterior direction, paying particular attention to the thoracic nota. The authors noted that the termite "appears" to be searching for cuticular clues of some sort on the other termite's exoskeleton. Termites under examination take a particular stance of lowering the side being examined and raising the other side. This behavior is believed to be

helpful in protecting the termite's tibia should attack ensue (Myles & Chang 1984). Attacks often followed such investigations in the form of bites to the abdomen, and chewing off of the antennae and legs.

Agonism among neotenics is common in the Kalotermitidae (Lenz 1985, Myles 1988), as demonstrated in *Pterotermes occidentis* Holmgren (Myles 1988) and *Kalotermes flavicollis* (Fabricius) (Ruppli 1969). Other families in the lower termites allow multiple neotenics to develop within a colony (Lenz 1985). Ruppli (1969) demonstrated that *K. flavicollis* neotenic aggression did not occur in those neotenics that had lost antennae, indicating that the receptors necessary for acquiring the cues releasing this behavior were found there. He also demonstrated a sexual difference in agonism among *K. flavicollis* neotenics. Female neotenics were demonstrated to attack more vigorously than males in eliminating other neotenics within the nest, especially when the victims were males (Ruppli 1969).

Nel (1968), working with alates of the harvester termite *Hodotermes mossambicus*, demonstrated that a period of isolation for mating pairs was necessary to induce aggressive behavior of the pair against other paired alates from the same parental colony. Length of isolation was positively correlated with degree of aggression in the pairs up to an isolation time of 220 hours. When pairs were allowed to excavate a nuptial chamber in the soil, the pair's aggression toward termites from the original colony increased. Nel (1968) reasoned that the isolation period provided the termites in the experiments was insufficient for the development of a distinct colony odor by the individual termite pairs, and thus ruled out the hypothesis of colony odor development as a reason for the observed agonism. He hypothesized that an alarm pheromone released by the termites was the releaser for the behavior. Unfortunately, no data were provided to support either of these suggestions. No evidence of a length of time necessary for developing a 'colony odor' has been established for termites, and the only evidence to support the presence of either a 'colony odor' or an 'alarm pheromone' was the fact that the animals were aggressive.

AGONISM IN LARVAL TERMITES

Some authors have drawn attention to the lack of agonistic behavior towards larval (first and second instar) termites (Andrews 1911, Thorne & Haverty 1991a). These authors indicated that larval termites are commonly investigated and subsequently ignored by non-nestmate conspecifics which react aggressively to older nestmates of the larvae. They suggested that the reason for this phenomenon is that larval termites lack whatever colony-specific cues exist for nestmate discrimi-

nation, and are therefore spared (Andrews 1911).

Errard (1994) worked with retention of kin recognition in the ants *Manica rubida* Latrielle and *Formica selysi* (Bondroit). Her results indicated that the ants were able to learn nestmate cues from ants of other species (allospecific), and were non-aggressive towards the familiar allospecifics even one year after separation. The author concluded that this may represent a template formation occurrence in the young ants, one which permits cues in the environment of the ant to be imbedded in the template as 'nestmate' even when those cues actually belong to another species. This raises the question of whether young termites acquire knowledge of 'nestmate' and 'non-nestmate' through genetic coding or through learning, possibly using a template as in ants. If the concept of 'nestmate' is a learned phenomenon in the developing termite, then the lack of aggression towards them is no longer a mystery. When two colonies abut one another, the young termites would be easily integrated into the colony that won the war, since they would still be capable of learning the cues of the victorious colony.

KIN RECOGNITION CUES

Colony odor.

Agonistic behavior in social insects is believed to be the result of a colony member's ability to recognize and differentiate between nestmates and non-nestmates (Wallis 1964). The term 'colony odor' has been used to describe chemical cues thought to be associated with individual colonies to enable members to make these distinctions (Wallis 1964). Past work has indicated that a colony odor may be important for colony recognition in honeybees and ants (Wallis 1964; Jutsum *et al.* 1979, Jaffe & Marcuse 1983). Wilson (1971) defined colony odor as "the odor found on the bodies of social insects which is peculiar to a given colony." When a species is said to use colony odor as a recognition component, an author is stating that the species' recognition method is at least partly chemically based. Some authors have proposed colony odor as a potential kin recognition cue in their work with termites (Thorne & Haverty 1991a). Using colonies of known relation, Adams (1991) showed that a cue referred to as 'colony odor' in *Microcerotermes arboreus* is a heritable characteristic. Jutsum *et al.* (1979) and Jaffe and Marcuse (1983) support colony odor as the method of colony recognition used by the ant species *Acromyrmex octospinosus* (Reich) and *Odontomachus bauri* Emery.

Cuticular hydrocarbons.

Studies of termite aggression have shown a tendency for termites to

examine one another with their antennae (Thorne & Haverty 1991a). This suggests cuticular hydrocarbons as possible cues for colony recognition (Clément 1986, Haverty & Thorne 1989, Thorne & Haverty 1991a, Bagnères *et al.* 1991, Su & Haverty 1991). However, this has been challenged in some species of termites, particularly *C. formosanus*, where colonies exhibiting very similar cuticular hydrocarbon profiles were shown to exhibit intercolonial agonism (Su & Haverty 1991). Recent work by Haverty *et al.* (1996) indicated that the cuticular hydrocarbon profiles of *C. formosanus* colonies on Oahu (Colonies B, F, G, and H in Shelton 1996) do contain enough variability to discriminate between castes within a colony, as well as between colonies within a geographical population. In this study, three caste profiles within the colonies were demonstrated to be significantly different: workers, soldiers, and nymphs/alates. Colonies were differentiated using their hydrocarbon components, but no correlation with agonistic patterns of the colonies was attempted (Haverty *et al.* 1996). Caste cuticular hydrocarbon profiles also indicated consistent seasonal variation within colonies, changing especially at the time of alate production and dispersal (Haverty *et al.* 1996). Cuticular hydrocarbon data have also been used as taxonomic characters for species and subspecies identification (Howard *et al.* 1978, 1982b, 1988; Haverty *et al.* 1988, 1990b, 1992; Haverty & Thorne 1989; Bagnères *et al.* 1990) and to trace the origins of populations of *C. formosanus* in the U.S. (Haverty *et al.* 1990a).

Other sources of intercolony variation.

Allozymes have been examined for correlation with agonistic behavior in Hawaiian colonies of *C. formosanus*, but very little variation was detected (Strong & Grace 1993). Wang and Grace (1995) recently resolved a greater number of variable loci in *C. formosanus*, however the authors did not attempt to correlate the loci variability with agonistic patterns of the colonies. Broughton and Grace (1994) found no mitochondrial DNA variation in the 10 Hawaiian colonies of *C. formosanus* they examined. The authors attributed this lack of variability to a possible genetic bottleneck due to low numbers of *C. formosanus* reproductives introduced into the islands. Allozyme variation among 45 *C. formosanus* colonies collected in Florida, Hawaii, and Louisiana was found to be extremely low by Korman and Pashley (1991). The authors suggest that the populations in Florida and Louisiana are not closely related to the Hawaiian population, a point also suggested by Haverty *et al.* (1990a) based upon cuticular hydrocarbons of the same colonies.

Multiple component hypothesis.

nism of colony recognition in *C. formosanus* including a chemical component, a behavioral component, and a digestive component. The mandibular gland may be a likely candidate for excretion of a chemical component, or colony odor. Chapman (1981) stated that the mandibular glands are present in the Isoptera, but their function is unknown. In an examination of trail pheromones in *Reticulitermes hesperus* Banks, Grace *et al.* (1995) suggested that sternal gland secretions did not contain colony-specific cues. While non-polar cuticular compounds have been investigated for intercolonial variation (Haverty *et al.* 1996), polar cuticular compounds have yet to be investigated in *C. formosanus* (Su & Haverty 1991). Su and Haverty also suggested that variable behavior patterns among colonies, particularly greeting behaviors, may act as releasers for agonistic behavior. Their suggestion of a digestive component of their hypothesis is similar to the chemical component discussed above. The key difference is the origin of the chemical emission. With a chemical component, the origin would be of genetic determination and an intrinsic or endogenous chemical factor. A digestive component would be dependent upon the environment, specifically the food sources available to the colony, and therefore be exogenous. Digestive components would arise from the foraging materials available to colonies, and variation in diet would be reflected in a variation in digestive emissions, either quantitatively or qualitatively. Thorne and Haverty (1991a) referred to this overall hypothesis as the "multiple stimulus hypothesis," since it stipulates that these three components could be used by the termites in conjunction or singly.

Shelton (1996) examined agonism between paired non-nestmates of exogenously similar laboratory colonies of *C. formosanus*. These pairings did not induce agonism between paired non-nestmates, supporting the use of one or more exogenous cues in *C. formosanus* kin recognition.

MANIPULATION OF AGONISTIC BEHAVIOR

A number of experimenters have manipulated agonistic behavior between termites (Andrews 1911; Dropkin 1946; Howick & Creffield 1980; Springhetti & Sapigni 1984, 1990). These manipulations have included attempts to 'wash away' chemical cues with water to produce a termite with no colony affiliation, and low temperature conditioning methods. Recent work by Cornelius and Grace (1994) demonstrated that *C. formosanus* can be induced to react aggressively using an extract of the predaceous sympatric ant species *Pheidole megacephala* (Fabricius).

Low temperature conditioning.

Dropkin (1946) examined the transference of host-specific gut symbionts between various species of kalotermitids after exposing the termites to low temperatures. In his study, drywood termite colonies maintained in the laboratory were chilled to immobility, and mixed with chilled colonies of other drywood (and one termopsid) termite species. Additional chilling attempts were sometimes necessary to reduce the fighting between the colonies once they were placed together. Using Dropkin's (1946) generic designations, he was able to maintain mixed colonies consisting of two *Kalotermes* spp., as well as *Kalotermes* spp. mixed with both a *Neotermes* sp. and a *Zootermopsis* sp. (Termopsidae) without visible agonism. Dropkin's (1946) work showed that for these species of termites, agonistic behavior could be suppressed for at least 230 days by prior low temperature conditioning. This study also demonstrated that movement and survival of gut protozoa between different species of drywood termites is possible. In some individuals of *Incisitermes schwarzi* (Banks), the gut fauna passed from *Neotermes jouteli* (Banks) through trophallaxis or proctodeal feeding were seen to displace the indigenous fauna in a mixed colony of the two species. Dropkin (1946) further suggested that this ease of transmission of gut fauna created an additional purpose for aggression in Isoptera: preventing trophallactic contact and inhibiting the movement of gut fauna from one species to another.

Modifying Dropkin's (1946) methodology for low temperature conditioning, Springhetti and Sapiigni (1984, 1990) investigated trophallaxis between termites of different families, *Kalotermes flavicollis* (Kalotermitidae) and *Reticulitermes lucifugus* Rossi (Rhinotermitidae). These authors demonstrated that a reduction in aggression was possible, although there were some "mixed colonies" in both Dropkin's (1946) and Springhetti and Sapiigni's (1984, 1990) studies that were still aggressive even after conditioning. Accounting for this variation, Springhetti and Sapiigni (1990) concluded that there may be variation within a colony for aggressive behavior, and for those termites (workers or soldiers) that are highly aggressive, the conditioning method was not sufficient to reduce agonism. Their studies demonstrated the ability for trophallactic transfer of tritiated amino acids from *K. flavicollis* to *R. lucifugus* and vice versa. They further suggested that the behavioral releaser cues for trophallaxis must be very similar for both species in order for trophallaxis to occur in this manner.

Howick and Creffield (1980) observed a reduction in aggressive behavior among non-nestmates of *Coptotermes acinaciformis* (Froggatt) following a similar low temperature manipulation. They used an

incubation regime of 3°C for a period of two hours, which enabled the formation of inter-colonially mixed groups of *C. acinaciformis*. Although the chilled termites were capable of remaining in non-nestmate groupings for short periods of time, only three of 16 groups survived for two weeks, and only two of the remaining three groups survived to 24 days. All of the combinations used three original colonies, and the surviving groups were composed of all the possible two-colony combinations of the three original colonies. The chilled combination that lasted two weeks had control (same colony combination unchilled) survival of only four days. Of the two groups surviving to 24 days, one combination's control survived to 26 days whereas the other combination's control only survived 10 days. This ruled out the possibility of survival resulting from a lack of intercolonial agonism between two of the combinations of colonies. Non-nestmate groupings were also found to consume significantly less wood than groups composed of nestmates.

Low temperature manipulation of intercolonial agonism in *C. formosanus* has been recently investigated by Shelton and Grace (1996). These authors demonstrated that a reduction in agonism between non-nestmates could be brought about using a low temperature conditioning regime of 3°C for one hour, provided that both non-nestmate groups were conditioned. This effect was temporary, lasting from 4-24 hours in *C. formosanus* foragers. Agonism in pairings of low temperature conditioned termites with unconditioned non-nestmates occurred with the conditioned termites attacking first, as well as more often, than their unconditioned opponents. Thus the low temperature conditioning effect was thought to have temporarily eliminated one or more kin recognition cues in the conditioned termites, making them unrecognizable to unconditioned non-nestmates. However, in paired conditioned non-nestmates the effect was temporary, providing evidence for the use of a kin recognition cue that is capable of being recovered over time, such as a glandular secretion (Shelton & Grace 1996).

Washing termites.

Andrews (1911) while working in Jamaica, made many observations on *Nasutitermes rippertii* (Rambur) (as *Termes rippertii* Rambur); Snyder (1949). He found that when *N. rippertii* workers were washed with water, they were attacked by both nestmates and non-nestmates. In his conclusions, he stated that he had removed some chemical that gave the workers their colony affiliation, making them aliens in their own nests.

Aggressive reactions to extracts.

Cornelius and Grace (1994) showed that hexane extracts of freshly

killed *Pheidole megacephala* (Fabricius) could be used to initiate aggressive behavior in soldiers of *C. formosanus*. The study demonstrated that *C. formosanus* soldiers reacted to the chemical components of the ant carcasses rather than physical cues, by using ant-extract treated nestmates of the termite soldier. The soldiers reacted differently to extracts of different ant species. *C. formosanus* soldiers avoided contact with *Ochetellus glaber* (Mayr) extracts and ignored extracts from two other ant species which were not known to inhabit termite galleries (Cornelius & Grace 1994). The authors stated that the aggressive reaction to *P. megacephala* may be a response to a more threatening enemy. This demonstrated that *C. formosanus* is capable of using chemical cues for reactions to Hymenopteran natural enemies, but responses to alien Isoptera were not investigated by these authors.

CIRCUMVENTION OF SPECIES RECOGNITION SYSTEMS

Even where a discrete species recognition mechanism does exist, circumvention of the mechanism is still possible (Kistner 1990). Social insect commensals use a variety of methods for integration into the colonies of their host species (Kistner 1990). The commensals remain in the host's nest and receive food via trophallaxis or feeding on the young of the host, as well as shelter and security from predation (Howard 1976; Howard *et al.* 1980, 1982a; Kistner 1990). The investigation of these termitophiles and myrmecophiles provide an avenue for the identification of the mechanism used by the host for species discrimination (Howard *et al.* 1980, 1982a; Kistner 1990). This is demonstrated by the staphylinid *Trichopsenius frosti* Seevers, which is capable of biosynthesizing the cuticular hydrocarbons found in its host *Reticulitermes flavipes* (Kollar) (Howard *et al.* 1980). *T. frosti* is also capable of exhibiting behaviors which induce grooming by female supplementary *R. flavipes* reproductives (Howard 1976). Two other staphylinids, *Xenistusa hexagonalis* Seevers and *Philoterme howardi* Kistner and Gut, are also capable of chemical mimicry, although only *X. hexagonalis* is known to biosynthesize cuticular hydrocarbons while living in nests of *Reticulitermes* spp. (Howard *et al.* 1982a).

CONTROL OF TERMITES USING AGONISTIC BEHAVIOR

Not all termitophiles living in the nests of termites are commensals. *Lomamyia latipennis* Carpenter (Neuroptera: Berothidae) is a termite predator living in the nests of its host, *Reticulitermes hesperus* Banks (Johnson & Hagen 1981). *Lomamyia latipennis* larvae use a volatile secretion produced at the tip of their abdomens to paralyze and feed upon all castes of *R. hesperus* (Johnson & Hagen 1981). The aggressive

allomone or volatile venom found in *L. latipennis* was demonstrated to be active across a filter paper barrier, suggesting potential for use in termite control.

Agonistic behavioral modification measures may have merit in the control of termites. French (1991) used the agonistic behavior of Australian *Coptotermes* spp. to the advantage of pest control operators by applying a dust toxicant to members of a conspecific or allospecific colony and then releasing them into the nest of the colony marked for control. Members of the nest attacked the newcomers, thereby transferring the toxin to themselves. Other authors have suggested the use of foragers from the target colony itself as vehicles for transmitting a toxin or pathogen to other colony members through trophallaxis and/or grooming (Grace & Zoberi 1992, Myles & Grace 1991, Myles *et al.* 1994, French 1994, Su 1994, Delate *et al.* 1995). The apparent absence of agonism among some *Reticulitermes* colonies (Grace 1996) implies that one could collect foragers from a single "farm" colony, treat them with a dust or topical toxicant as suggested by Myles and Grace (1991) and Myles *et al.* (1994), and release them into entirely different colonies.

Thorne and Haverty (1991a) stated that "any stimulus that aggravates termites is potentially useful in termite control." Although it is difficult to define this potential in a more concrete fashion, development of chemicals to confuse or repel termites is one possible application. However, the use of agonistic behavior, or identification and use of the actual cues recognized by the termites themselves, to delineate specific termite colonies (Thorne & Haverty 1991b; Jones 1990, 1993) may also be of value in assessing the efficacy of baits applied for subterranean termite control. In genera such as *Heterotermes*, where intercolony agonism is common, behavioral assays offer a quick means of determining whether multiple termite colonies are present at a particular location (Jones 1990, 1993). Undoubtedly, as agonistic behavior is better understood, practical applications of our new understanding will be more apparent.

ACKNOWLEDGMENTS

We are grateful to Julian R. Yates III, M. Lee Goff, Marshall W. Johnson (Dept. of Entomology, University of Hawaii), and an anonymous reviewer for helpful comments on early drafts of the manuscript. Partial funding was provided by McIntire Stennis and by USDA-ARS Specific Cooperative Agreements No. 58-6615-9-012 and 58-6615-4-037. This is Journal Series No. 4191 of the Hawaii Institute of Tropical Agriculture and Human Resources.

REFERENCES

- Adams, E.S. 1991. Nest-mate recognition based on heritable odors in the termite *Microcerotermes arboreus*. Proc. Nat. Acad. Sci. 88: 2031-2034.
- Andrews, E.A. 1911. Observations on termites in Jamaica. J. Animal Behavior 1: 193-228.
- Bagnères, A.G., J.-L. Clément, M.S. Blum, R.F. Severson, C. Joulie, and C. Lange. 1990. Cuticular hydrocarbons and defensive compounds of *Reticulitermes flavipes* (Kollar) and *R. santonensis* (Feytaud): polymorphism and chemotaxonomy. J. Chem. Ecol. 16: 3213-3244.
- Bagnères, A.G., A. Killian, J.-L. Clément, and C. Lange. 1991. Interspecific recognition among termites of the genus *Reticulitermes*: evidence for a role for the cuticular hydrocarbons. J. Chem. Ecol. 17: 2397-2420.
- Binder, B.F. 1988. Intercolonial aggression in the subterranean termite *Heterotermes aureus* (Isoptera: Rhinotermitidae). Psyche 95: 123-137.
- Blum, M.S., T.H. Jones, D.F. Howard, and W.L. Overal. 1982. Biochemistry of termite defenses: *Coptotermes*, *Rhinotermes*, and *Cornitermes* species. Compar. Biochem. Physiol. 71B: 731-733.
- Broughton, R.E., and J.K. Grace. 1994. Lack of mitochondrial DNA variation in an introduced population of the Formosan subterranean termite (Isoptera: Rhinotermitidae). Sociobiology 24: 121-126.
- Chapman, R.F. 1981. The insects structure and function. Third Edition. Harvard University Press, Cambridge. Pp. 871-876.
- Chuah, C.H., S.H. Goh, and Y.P. Tho. 1990. Chemical defense secretions of some species of Malaysian Rhinotermitidae (Isoptera: Rhinotermitidae). J. Chem. Ecol. 16: 685-692.
- Clément, J.-L. 1986. Open and closed societies in *Reticulitermes* termites (Isoptera: Rhinotermitidae): geographic and seasonal variations. Sociobiology 11: 311-323.
- Clément, J.-L., M. LeMaire, P. Nagnan, P. Escoubas, A.G. Bagnères, and C. Joulie. 1988. Chemical ecology of European termites of the genus *Reticulitermes* allomones, pheromones, and kairomones. Sociobiology 14: 165-174.
- Cornelius, M.L., and J.K. Grace. 1994. Behavioral responses of the Formosan subterranean termite (Isoptera: Rhinotermitidae) to semiochemicals of seven ant species. Environ. Entomol. 23: 1524-1528.
- Cornelius, M.L., and J.K. Grace. 1995. Laboratory evaluations of interactions of three ant species with the Formosan subterranean termite (Isoptera: Rhinotermitidae). Sociobiology 26:291-298.
- Delaplane, K.S. 1991. Tests for intraspecific agonism in a Louisiana population of *Coptotermes formosanus* (Isoptera: Rhinotermitidae). J. Entomol. Sci. 26: 357-359.
- Delate, K.M., J.K. Grace, and C.H.M. Tome. 1995. Potential use of pathogenic fungi in baits to control the Formosan subterranean termite (Isoptera: Rhinotermitidae). J. Appl. Entomol. 119: 429-433.
- Dropkin, V.H. 1946. The use of mixed colonies of termites in the study of host-symbiont relations. J. Parasitol. 32: 247-251.

- Emerson, A.E. 1933. Conditioned behavior among termites (Isoptera). *Psyche* 40: 125-129.
- Errard, C. 1994. Long-term memory involved in nestmate recognition in ants. *Anim. Behav.* 48: 263-271.
- French, J.R.J. 1991. Baits and foraging behavior of Australian species of *Coptotermes*. *Sociobiology* 19: 171-186.
- French, J.R.J. 1994. Combining physical barriers, bait and dust toxicants in future strategies for subterranean termite control (Isoptera). *Sociobiology* 24: 77-91.
- Goh, S.H., C.H. Chuah, J. Vadiveloo, and Y.P. Tho. 1990. Soldier defense secretions of Malaysian free-ranging termite of the genus *Lacessitermes* (Isoptera, Nasutitermitinae). *J. Chem. Ecol.* 16: 619-630.
- Grace, J.K. 1992. Termite distribution, colony size, and potential for damage. In: *Proceedings of the national conference on urban entomology*. W.H. Robinson, ed. College Park, Maryland. Pp. 67-76.
- Grace, J.K. 1996. Absence of overt agonistic behavior in a northern population of *Reticulitermes flavipes* (Isoptera: Rhinotermitidae). *Sociobiology* 28(1): 103-110.
- Grace, J.K., A. Abdallay, and K.R. Farr. 1989. Eastern subterranean termite (Isoptera: Rhinotermitidae) foraging territories and populations in Toronto. *Can. Entomol.* 121: 551-556.
- Grace, J.K., and M.H. Zoberi. 1992. Experimental evidence for transmission of *Beauveria bassiana* by *Reticulitermes flavipes* workers (Isoptera: Rhinotermitidae). *Sociobiology* 20: 23-28.
- Grace, J.K., D.L. Wood, I. Kubo, and M. Kim. 1995. Behavioral and chemical investigation of trail pheromone from the termite *Reticulitermes hesperus* Banks (Isoptera: Rhinotermitidae). *J. Appl. Entomol.* 119: 501-505.
- Haverty, M.I. 1977. The proportion of soldiers in termite colonies: a list and a bibliography (Isoptera). *Sociobiology* 2: 199-216.
- Haverty, M.I. 1979. Soldier production and maintenance of soldier proportions in laboratory experimental groups of *Coptotermes formosanus* Shiraki. *Ins. Sociaux* 26: 69-84.
- Haverty, M.I., M. Page, L.J. Nelson, and G.J. Blomquist. 1988. Cuticular hydrocarbons of dampwood termites, *Zootermopsis*: intra- and intercolony variation and potential as taxonomic characters. *J. Chem. Ecol.* 14: 1035-1058.
- Haverty, M.I., and B.L. Thorne. 1989. Agonistic behavior correlated with hydrocarbon phenotypes in dampwood termites, *Zootermopsis* (Isoptera: Termopsidae). *J. Ins. Behav.* 2: 523-543.
- Haverty, M.I., L.J. Nelson, and M. Page. 1990a. Cuticular hydrocarbons of four populations of *Coptotermes formosanus* Shiraki in the United States. *J. Chem. Ecol.* 16: 1635-1647.
- Haverty, M.I., B.L. Thorne, and M. Page. 1990b. Surface hydrocarbon components of two species of *Nasutitermes* from Trinidad. *J. Chem. Ecol.* 16: 2441-2450.
- Haverty, M.I., L.J. Nelson, B.L. Thorne, M.S. Collins, J.P.E.C. Darlington, and

- M. Page. 1992. Cuticular hydrocarbons for species determination of tropical termites. *In*: Proceedings, Session on Tropical Forestry for People of the Pacific, XVII Pacific Science Congress (May 1991), USDA Gen. Tech. Rep. PSW-GTR-129: 58-66.
- Haverty, M.I., and J.K. Grace. 1993. How similar are colonies of the formosan subterranean termite? Evidence from hydrocarbon and enzyme studies from Hawaii and the mainland United States. Poster Abstract. *In*: Proceedings of the First International Conference on Insect Pests in the Urban Environment. Wildey, K.B., and W.H. Robinson, eds. BPCC Wheatons Ltd. Exeter. P. 471.
- Haverty, M.I., J.K. Grace, L.J. Nelson, and R.T. Yamamoto. 1996. Intercaste, intercolony, and temporal variation in cuticular hydrocarbons of *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae). *J. Chem. Ecol.*, in press.
- Howard, R.W. 1976. Observations on behavioral interactions between *Trichopentus frosti* Seevers (Coleoptera: Staphylinidae) and *Reticulitermes flavipes* (Kollar) (Isoptera: Rhinotermitidae). *Sociobiology* 2: 189-192.
- Howard, R.W., C.A. McDaniel, and G.J. Blomquist. 1978. Cuticular hydrocarbons of the eastern subterranean termite, *Reticulitermes flavipes* (Kollar) (Isoptera: Rhinotermitidae). *J. Chem. Ecol.* 4: 233-245.
- Howard, R.W., C.A. McDaniel, and G.J. Blomquist. 1980. Chemical mimicry as an integrating mechanism: cuticular hydrocarbons of a termitophile and its host. *Science* 210: 431-433.
- Howard, R.W., C.A. McDaniel, and G.J. Blomquist. 1982a. Chemical mimicry as an integrating mechanism for three termitophiles associated with *Reticulitermes virginicus* (Banks). *Psyche* 89: 157-167.
- Howard, R.W., C.A. McDaniel, D.R. Nelson, G.J. Blomquist, L.T. Gelbaum, and L.H. Zalkow. 1982b. Cuticular hydrocarbons of *Reticulitermes virginicus* (Banks) and their role as potential species- and caste-recognition cues. *J. Chem. Ecol.* 8: 1227-1239.
- Howard, R.W., B.L. Thorne, S.C. Levings, and C.A. McDaniel. 1988. Cuticular hydrocarbons as chemotaxonomic characters for *Nasutitermes corniger* (Motschulsky) and *N. ephratae* (Holmgren) (Isoptera: Termitidae). *Ann. Entomol. Soc. Am.* 81: 395-399.
- Howick, C.D., and J.W. Creffield. 1980. Intraspecific antagonism in *Coptotermes acinaciformis* (Froggatt) (Isoptera: Rhinotermitidae). *Bull. Ent. Res.* 70: 17-23.
- Howse, P.E. 1965. On the significance of certain oscillatory movements of termites. *Ins. Sociaux* 12: 335-346.
- Jaffe, K., and M. Marcuse. 1983. Nestmate recognition and territorial behaviour in the ant *Odontomachus bauri* Emery (Formicidae: Ponerinae). *Ins. Sociaux* 30: 466-481.
- Johnson, J.B., and K.S. Hagen. 1981. A neuropterous larva uses an allomone to attack termites. *Nature* 289: 506-507.
- Jones, S.C. 1990. Delineation of *Heterotermes aureus* (Isoptera: Rhinotermitidae) foraging territories in a sonoran desert grassland. *Environ. Entomol.* 19:

1047-1054.

- Jones, S.C. 1993. Field observations of intercolony aggression and territory changes in *Heterotermes aureus* (Isoptera: Rhinotermitidae). *J. Ins. Behav.* 6: 225-236.
- Jutsum, A.R., T.S. Saunders, and J.M. Cherrett. 1979. Intraspecific aggression in the leaf-cutting ant *Acromyrmex octospinosus*. *Animal Behav.* 27: 839-844.
- Kistner, D.H. 1990. The integration of foreign insects into termite societies or why do termites tolerate foreign insects in their societies? *Sociobiology* 17: 191-215.
- Kofoid, C.A. 1934. *Termites and termite control*. Second Edition, revised. University of California Press, Berkeley. 795 pp.
- Korman, A.K., and D.P. Pashley. 1991. Genetic comparisons among U.S. populations of Formosan subterranean termites. *Sociobiology* 19: 41-50.
- Krebs, J.R., and N.B. Davies. 1993. *An introduction to behavioural ecology*. Third Edition. Blackwell Scientific Publications. London. 420 pp.
- Lai, P.-Y. 1977. Biology and ecology of the Formosan subterranean termite, *Coptotermes formosanus*, and its susceptibility to the entomogenous fungi, *Beauveria bassiana* and *Metarhizium anisopliae*. Ph.D. dissertation, University of Hawaii at Manoa, Honolulu.
- LeMaire, M., P. Nagnan, J.-L. Clement, C. Lange, L. Peru, and J.-J. Basselier. 1990. Geranylinalool (diterpene alcohol) an insecticidal component of pine wood and termites (Isoptera: Rhinotermitidae) in four European ecosystems. *J. Chem. Ecol.* 16: 2067-2079.
- Lenz, M. 1985. Is interspecific variability of lower termite neotenic numbers due to adaptive thresholds for neotenic elimination? - Considerations from studies on *Porotermes adamsoni* (Froggatt) (Isoptera: Termopsidae). In: *Caste Differentiation in Social Insects*. Watson, J.A.L., B.M. Okot-Kotber, and CH. Noirot, eds. Pergamon Press. Oxford. Pp. 125-145.
- Levings, S.C., and E.S. Adams. 1984. Intra- and interspecific territoriality in *Nasutitermes* (Isoptera: Termitidae) in a Panamanian mangrove forest. *J. Anim. Ecol.* 53: 705-714.
- Myles, T.G., and F. Chang. 1984. The caste system and caste mechanisms of *Neotermes connexus* (Isoptera: Kalotermitidae). *Sociobiology* 9: 226-228.
- Myles, T.G. 1988. Resource inheritance in social evolution from termites to man. In: *The ecology of social behavior*. C.N. Slobodchikoff, ed. Academic Press, Inc., Berkeley. Pp. 379-423.
- Myles, T.G., A. Abdallay, and J. Sisson. 1994. 21st century termite control. *Pest Control Technology* (March 1994). Pp. 64-108.
- Myles, T.G. & J.K. Grace. 1991. Behavioral ecology of the eastern subterranean termite in Ontario as a basis for control. *Proc. Technol. Transfer Conf.*, Vol. II, *The Multi-Media Approach: Integrated Environmental Protection*. Ontario Ministry of the Environment, Toronto. pp. 547-554.
- Myles, T.G., and W.L. Nutting. 1988. Termite eusocial evolution: a re-examination of Bartz's hypothesis and assumptions. *Quart. Rev. Biol.* 63:1-23.

- Nel, J.J.C. 1968. Aggressive behaviour of the harvester termites *Hodotermes mossambicus* (Hagen) and *Trinervitermes trinervoides* (Sjöstedt). *Ins. Sociaux* 15: 145-156.
- Pearce, M.J., R.H. Cowie, A.S. Pack, and D. Reavey. 1990. Intraspecific aggression, colony identity and foraging distances in Sudanese *Microtermes* spp. (Isoptera: Termitidae: Macrotermitinae). *Ecol. Entomol.* 15: 71-77.
- Prestwich, G.D. 1984. Defense mechanisms of termites. *Ann. Rev. Entomol.* 29: 201-232.
- Prestwich, G.D. 1988. The chemicals of termite societies (Isoptera). *Sociobiology* 14: 175-186.
- Price, P.W. 1984. *Insect ecology*. Second Edition. John Wiley & Sons. New York. 607 pgs.
- Quennedey, A., and J. Deligne. 1975. L'arme frontale des soldats de termites. I. Rhinotermitidae. *Ins. Sociaux* 22: 243-267.
- Roisin, Y., C. Everaerts, J.M. Pasteels, and O. Bonnard. 1990. Caste-dependent reactions to soldier defensive secretion and chiral alarm/recruitment pheromone in *Nasutitermes princeps*. *J. Chem. Ecol.* 16: 2865-2875.
- Ruppli, V.E. 1969. Die Elimination überzähliger Ersatzgeschlechtstiere bei der Termiten *Kalotermites flavicollis* (Fabr.). *Ins. Sociaux* 16: 235-248.
- Scheffrahn, R.H., L.K. Gaston, J.J. Sims, and M.K. Rust. 1983. Identification of the defensive secretion from soldiers of the north american termite, *Amitermes wheeleri* (Desneux) (Isoptera: Termitidae). *J. Chem. Ecol.* 9: 1293-1305.
- Scheffrahn, R.H., N.-Y. Su, J.J. Sims, and A.M.K. El-Sayed. 1987. Composition and ant-repellency of the soldier defensive secretion of the palearctic termite, *Amitermes desertorum* (Isoptera: Termitidae). *Sociobiology* 13: 75-82.
- Scheffrahn, R.H., M.K. Rust, J.P. Toth, and N.-Y. Su. 1988. Soldier defensive secretions of two rare nearctic desert termite species. *Biochem. System. Ecol.* 16: 213-216.
- Shelton, T.G. 1996. Factors affecting colony recognition in *Coptotermes formosanus* Shiraki (Isopter: Rhinotermitidae). M.S. thesis, University of Hawaii at Manoa, Honolulu.
- Shelton, T.G., and J.K. Grace. 1996. Impact of low temperature conditioning on intercolonial agonism in *Coptotermes formosanus* Shiraki. *Ins. Behav., in review*.
- Snyder, T.E. 1949. *Catalog of the termites (Isoptera) of the world*. Smithsonian Institution, Washington, D.C.
- Springhetti, A., and T. Sapigni. 1984. Are there trophallactic exchanges among pseudergates of different species of termites? (Isoptera: Rhinotermitidae and Kalotermitidae). *Sociobiology* 9: 1-7.
- Springhetti, A., and T. Sapigni. 1990. Trophallaxis between *Reticulitermes lucifugus* and *Kalotermites flavicollis* (Isoptera). *Sociobiology* 17: 245-258.
- Strong, K.L., and J.K. Grace. 1993. Low allozyme variation in Formosan subterranean termite (Isoptera: Rhinotermitidae) colonies in Hawaii. *Pan-Pac. Entomol.* 69: 51-56.

- Stuart, A.M. 1967. Alarm, defense, and construction behavior relationships in termites (Isoptera). *Science* 156: 1123-1125.
- Su, N.-Y., and J.P. LaFage. 1987a. Effects of soldier proportion on the wood-consumption rate of the Formosan subterranean termite (Isoptera: Rhinotermitidae). *Sociobiology* 13: 145-151.
- Su, N.-Y., and J.P. LaFage. 1987b. Initiation of worker-soldier trophallaxis by the Formosan subterranean termite (Isoptera: Rhinotermitidae). *Ins. Sociaux* 34: 229-235.
- Su, N.-Y., and R.H. Scheffrahn. 1988a. Intra- and interspecific competition of the Formosan and the Eastern subterranean termite: evidence from field observations (Isoptera: Rhinotermitidae). *Sociobiology* 14: 157-164.
- Su, N.-Y., and R.H. Scheffrahn. 1988b. Foraging population and territory of the Formosan subterranean termite (Isoptera: Rhinotermitidae) in an urban environment. *Sociobiology* 14: 353-359.
- Su, N.-Y., and M.I. Haverty. 1991. 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. *J. Ins. Behav.* 4: 115-128.
- Su, N.-Y., P.M. Ban, and R.H. Scheffrahn. 1993. Foraging populations and territories of the eastern subterranean termite (Isoptera: Rhinotermitidae) in southeastern Florida. *Environ. Entomol.* 22: 1113-1117.
- Su, N.-Y. 1994. Field evaluation of a Hexaflumeron bait for population suppression of subterranean termites (Isoptera: Rhinotermitidae). *J. Econ. Entomol.* 87: 389-397.
- Thorne, B.L. 1982. Termite-termite interactions: workers as an agonistic caste. *Psyche* 89: 133-150.
- Thorne, B.L., and M.I. Haverty. 1991a. A review of intracolony, intraspecific, and interspecific agonism in termites. *Sociobiology* 19: 115-145.
- Thorne, B.L., and M.I. Haverty. 1991b. An assessment of the potential uses of agonistic behaviors in termite control. *In: Proceedings of the symposium on current research on wood-destroying organisms and future prospects for protecting wood in use.* USDA Gen. Tech. Rep. PSW-128: 24-27.
- Tranillo, J.F.A., and S.N. Beshers. 1985. Species-specific alarm/recruitment responses in a neotropical termite. *Naturwiss.* 72: 491-492.
- Valterova, I., J. Vrkoc, and T. Norin. 1993. The enantiomeric composition of monoterpene hydrocarbons in the defensive secretions of *Nasutitermes* termites (Isoptera): inter- and intraspecific variations. *Chemoecol.* 4: 120-123.
- Wallis, D.I. 1964. Aggression in social insects. *In: The natural history of aggression.* J.D. Carthy and F.J. Ebeling, eds. Academic Press, New York. Pp. 15-22.
- Wang, J. & J.K. Grace. 1995. Using a genetic marker (MDH-1) to study genetic structure in colonies of *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae). *In: Hawaii agriculture preparing for growth. Conference proceedings.* College of Tropical Agriculture and Human Resources, University of Hawaii, Honolulu.

- Wheeler, W.M. 1928. The social insects, their origin and evolution. Harcourt, Brace and Company. New York. 378 pp.
- Wilson, E.O. 1971. The insect societies. Belknap/Harvard Press. Cambridge. 548 pp.
- Wilson, E.O. 1975. Sociobiology. Belknap/Harvard Press. Cambridge. 697 pp.
- Zimmerman, E.C. 1948. Order Isoptera. *In*: Insects of Hawaii, Volume 2: Apterygota to Thysanoptera inclusive. University of Hawaii Press, Honolulu. pp. 159-190.

