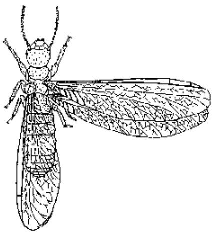

# An individual based model examining the emergence of cooperative defense in a social insect colony.

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Abstract:

In this paper we use an agent-based model to simulate the expression of defensive behavior among individual workers within colonies of termites. We predict there are three components to successful defensive behavior: the variation in recognition cues among different colonies, signaling among individuals, and variation in response thresholds. We provide background information on the behaviors studied, as well as references that support the parameters of our model. Expression in defensive behavior varies among different species of subterranean termites. Some species show no defensive behavior at all, which we attempt to explain with the model. There is also a strong difference in expression of inter- and intraspecific defensive behavior, which we attempt to explain with the model. The results suggest that if cue difference is not significantly variable, and response thresholds are high, defensive behavior will not be expressed. Under these situations, social signaling becomes increasingly important. We compare these results with previously published laboratory bioassays and show that the results are analogous to what is seen in the laboratory. The model provides a simple mechanistic description of how defensive behavior emerges from simple worker-to-worker interactions, and explains why a group effect is found in many laboratory bioassays. We also discuss further laboratory experiments to test the predictions of the model.

## Nestmate Recognition:

Nestmate recognition, the ability to tell colonymates from non-colonymates, in social insects is an important mechanism for kin selection (Fletcher & Michener 1987). Concurrently, nestmate recognition allows individuals to determine who belongs to the colony and who doesn't, thereby preventing usurpation of nesting and food resources, and social parasitism.

Recognition behaviors include both positive and negative interactions. Positive interactions, accepting related individuals, include such things as allogrooming (grooming other individuals within the colony), positive assortment of related individuals, or increased antennation time (time spent "smelling" other individuals with their antennae). Because it is easier to score in a laboratory or field setting, negative interactions, rejecting alien individuals, is the most commonly examined recognition behavior. Defensive behavior can include biting, attacking or repulsion. In bees it can result in stinging, and in ants the lowering of the gaster and spraying of formic acid. In termites, defensive behavior consists of biting, and then killing an alien worker.

## Defensive Behavior in Termites:

In subterranean termites (Isoptera:Rhinotermitidae:*Reticulitermes spp.*), the expression of defensive behavior varies according to species. In the Eastern subterranean termite

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(*Reticulitermes flavipes*), intraspecific (among colonies in the same species) defensive behavior is frequently absent (Bulmer & Traniello 2002, Polizzi & Forschler 1998), although interspecific (among colonies of different species) defensive behavior is present (Polizzi & Forschler 1998). Workers in some populations of *R. flavipes* do not recognize and act defensively against other workers known to be from different colonies, but *can* recognize workers from different species. In the Western subterranean termite, both conspecific and allospecific defensive behavior is present in all populations studied (Haverty *et al*, 1999), but we have also witnessed a group effect. One on one dyadic interactions do not result in outright aggression and death (Delphia *et al*, 2002), while ten on ten (Haverty *et al*, 1999) and ten on one does (Copren 2003). This suggests that social interactions may be important in defensive behavior. These differences are found in some species of ants as well (Boulay & Lenoir 2001, Lenoir *et al*, 2001).

If defensive behavior is necessary to defend the colony against potential competitors, why do some species not exhibit it? A loss of recognition ability is seen in the invasive argentine ant. Its native habitat consists of many colonies that express defensive behavior against one another (Tsutsui *et al*, 2000), but in its introduced habitat it shows no defensive behavior against neighboring colonies (Holway *et al*, 1998). In fact, all colonies are so cooperative they form a giant super colony. Although this is not an evolutionarily stable strategy, because workers are acting altruistically towards individuals they are not related to, ecologically it appears to be a successful. Why and how this evolves is currently being debated. The leading hypothesis is that these organisms underwent a genetic bottleneck, reducing genetic variability (Tsutsui *et al*, 2000). Assuming recognition cues are genetically determined, there was a loss of genetic diversity, and, hence, a loss of recognition behavior. This allows smaller colonies to join together and form one, giant super-colony.

Is it possible this could explain the variation in defensive behavior in subterranean termites? There is evidence that *R. flavipes* has been transported and introduced around the world (Marini & Mantovani 2002, Jenkins *et al*, 2001). There is also evidence that recognition cues in termites and other ants have a genetic component (Beye *et al*, 1998, Adams 1991). Therefore, we use this hypothesis to propose one of the parameters of our model. This parameter is cue difference, and is explained below.

Recognition Cues:

Nestmate recognition is argued to function by "phenotype matching" (Lacy & Sherman 1983). Individuals compare the phenotype of potential partners with an inner template, checking for similarities or dissimilarities. The inner template may be learned by learning one's own template (the so-called "armpit effect") or through learning the colony's odor. Similarities may come from genetically determined cues, or from the environment such as the nest or shared food. Different environmental situations are thought to favor the evolution of more genetically or environmentally determined traits (Lehmann & Perrin 2002.). Different species may use different methods. Likely, in most species there is an environmental and genetic component for recognition.

In social insects, cuticular hydrocarbons are the leading contender as recognition cues (Haverty *et al*, 1999, Ruther *et al*, 2002, Breed 1998). Cuticular hydrocarbons are waxy lipids found on the exoskeleton of insects that prevent them from desiccation. Hydrocarbon composition can vary from species to species, as well as from colony to colony. Typically, large quantitative differences are found between species in hydrocarbon composition (Page, *et al* 2002, Haverty & Nelson 1997). There can be quantitative difference in hydrocarbon profiles within a species from colony to colony (Kaib et al 2002), but frequently, there are only qualitative differences. Each colony has the same hydrocarbons, but varies in subtle differences of the amount of each hydrocarbon (Haverty & Nelson 1997). Therefore, we argue that cue difference between species is larger than within a species. In the model we consider large cue differences to be analogous to interspecific interactions, and small differences to be analogous to intraspecific interactions.

## Importance of Social Facilitation:

Social facilitation and a group effect have been shown to be important in longevity of termites (Miramontes & DeSouza 2002), but not in nestmate recognition. Boulay & Lenoir (2002) show that in the ant, *Camponotus fellah*, (a species of Carpenter ant) social interaction is required to maintain recognition ability. From these studies, we hypothesize that social facilitation is important for termite recognition as well. We argue that each worker termite has an innate response threshold that can be further stimulated with social signaling.

In our model, we hypothesize that individuals release a chemical or behavioral cue when attacked, which lowers the response thresholds of its colonymates. No such chemical has been isolated in termites to date, but observations suggest one exists. When termites are attacked, they often defecate in defense (personal observation of K. Copren). It is known that the bacterial fauna in the hindgut of termites plays a role in recognition behavior (Matsuura 2001). Therefore, it is reasonable to hypothesize that there may be a chemical cue released when a worker is attacked, which may have a stimulatory effect on other workers in that colony. In contrast, the signal may be behavior. Workers are known to tap their bodies on the nest substrate and send vibrational cues to other colony-mates when agitated (Kirchner *et al*, 1994). We argue that signaling may occur and be a mechanism for social facilitation.

We suggest that recognition, and hence the expression of defensive behavior, is based both on the amplitude of the cue difference (which may also be considered genetic distance if cues are genetically determined) between workers in different colonies, variation in individual response thresholds, and social facilitation (signaling). We predict that a very high cue difference, such as is found in interspecific cuticular hydrocarbon profiles, will provide enough stimulus that social facilitation may not be necessary. However, in intraspecific interactions, where hydrocarbon profiles are only qualitatively different, we predict that social facilitation will be more important. Therefore, we analyze the interaction of these three parameters (cue difference, response threshold variation, and signaling) in a model to determine the mechanistic basis responsible for laboratory observations. Using an agent-based model allows us to vary these parameters simultaneously, close to intractable with a typical analytical model. To our knowledge, this is the first model to examine the effect of social interactions on colony defensive behavior.

## An Agent-Based Model:

In order to investigate the emergence of cooperative defense in a social insect colony *in silica*, we developed an agent-based model (Bonabeau *et al* 1998, Miramontes & DeSouza 2002) using the StarLogo[1] software package (Figure 1). Our model consisted of individual agents, representing termites, divided into two sets – a defending colony and an intruding colony with some magnitude of cue difference between them. The agents interacted on a bounded square grid according to a set of simple behavioral rules based on observations of real termites.

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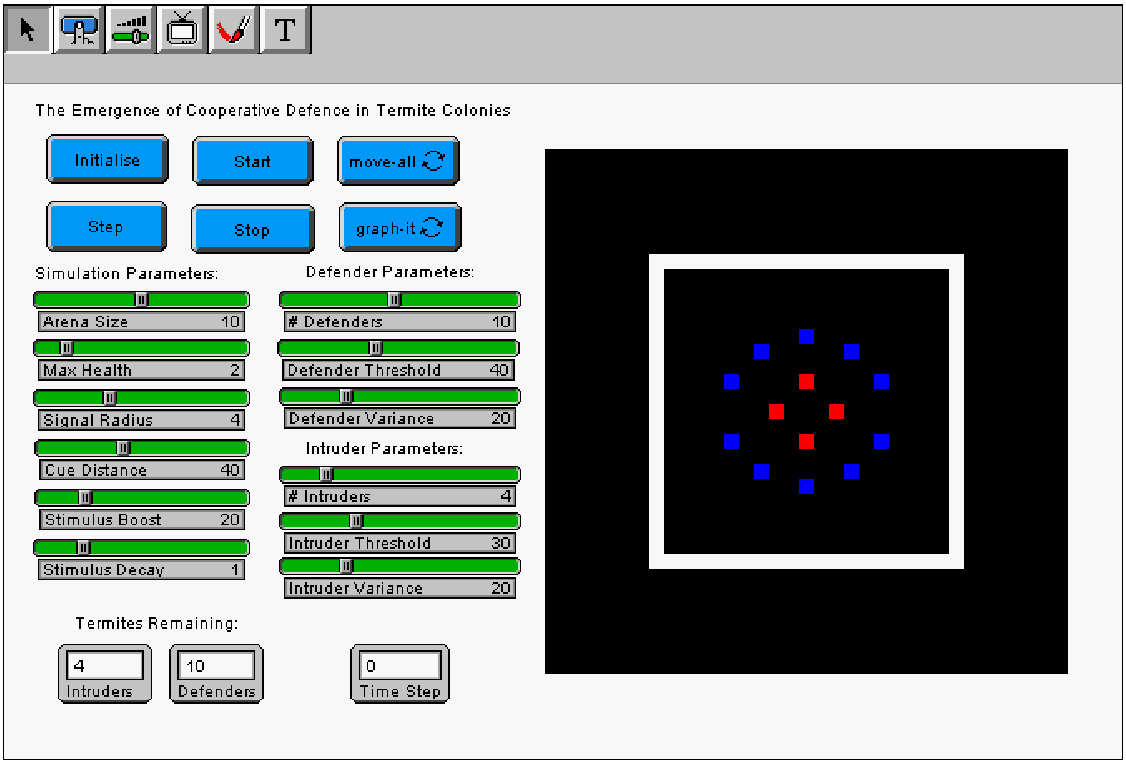
[1] StarLogo can be obtained from http://www.media.mit.edu/starlogo/

Agents moved randomly on the grid, occasionally encountering a termite from the foreign colony. At this point, each of the termites attacked the other with a probability based upon its level of aggressiveness and the amount of stimulation it had received. The occurrence of an attack resulted in a signal being transmitted to other agents in the vicinity, raising their level of stimulation. This model was used to investigate the effects of cue difference, signal strength and response threshold on the time taken for the defending colony to eliminate an intruder.



The Emergence of Cooperative Defence in Termite Colonies

Simulation Parameters:

Arena Size 10

Max Health 2

Signal Radius 4

Cue Distance 40

Stimulus Boost 20

Stimulus Decay 1

Defender Parameters:

Defenders 10

Defender Threshold 40

Defender Variance 20

Intruder Parameters:

Intruders 4

Intruder Threshold 30

Intruder Variance 20

Termites Remaining:

4 Intruders

10 Defenders

0 Time Step

**Figure 1: The StarLogo interface. The white square indicates the boundary of the arena, the blue agents are the defending colony and the red agents are the intruding colony. The sliding bars on the left allow the various simulation parameters to be modified.**

Parameters:

The distance between the two colonies was represented by a global cue difference variable. All individuals within a colony were completely related (i.e. there was no intraspecific cue difference).

Several state variables were defined for the agents. Each agent had a threshold, representing its innate level of aggressiveness - an agent with a low threshold would attack with less provocation than an agent with a high threshold. An individual agent's threshold was fixed across the course of an experiment. The threshold of each individual was determined randomly, based on a specified mean and variance for each colony. The variation of threshold levels within a colony could be important for the coordination of defense, as individuals with low thresholds, who were more likely to attack an intruder, could send signals raising the stimulus intensity level of the members of the colony with higher thresholds[1]. The stimulus intensity level of each agent represented the amount of 'aggravation' it was currently experiencing. It was initially set equal to the cue difference between the two colonies and updated at each time step. An agent's stimulus level could increase in response to attacks occurring in its vicinity and was also subject to a slow decay constant. The stimulus intensity at each time step was given by

$$s_i(t+1) = s(t)_i + \sum_j \sigma_{ij} - \delta$$

where $s_i(t)$ the stimulus level of agent $i$ at time $t$, $\sigma_{ij}$ is the strength of the stimulus increasing signal from agent $j$ , summed over all the agents in the vicinity and $\delta$ is the stimulus decay constant. Each agent's initial stimulus intensity level, $s_i(t=0)$, was the cue difference between the two colonies. A stimulus decay rate of $\delta = 0.1$ was typically used in these experiments

When an attack occurred, a signal was emitted in a circular area centered on the cell in which the attack took place. This signal had the effect of raising the level of stimulus of the agents within the signal radius by an amount proportional to their distance from the attack. The signal strength was given by

$$\sigma_{ij} = \begin{cases} \dfrac{\beta}{d_{ij}} & \text{if } 0 < d_{ij} < d_{\max} \\ 0 & \text{if } d_{ij} \geq d_{\max} \end{cases}$$

where $\sigma_{ij}$ is the stimulus increasing signal received by agent $i$ from agent $j$, $\beta$ is the initial signal strength, $d_{ij}$ is the distance between agents $i$ and $j$ and $d_{\max}$ is the signal radius. Both the radius of the signal and its strength could be varied. A signal radius ($d_{\max}$) of 4 was generally used in these experiments and the signal strength ($\beta$) was varied between 0 and 40.

Finally each agent had a health variable tracking the number of times it had been attacked. A global parameter defined the number of attacks an agent could withstand before dying. Each agent generally started with a health of 2 in these experiments (i.e. they could withstand two attacks before dying).

Simulations:

The agents were initialized in concentric circles, the inner circle representing the intruding colony and the outer circle the defending colony. This arrangement reflects the situation in *in vitro* experiments, where intruding termites are placed in the center of a petri dish containing the defending colony. The agents moved randomly across the constrained grid and interacted with one another whenever two agents entered the same cell. At this point, there was a chance, based upon the level of their threshold and stimulus, that each would attack the other. The probability of an agent attacking was based upon the simple model of response thresholds developed by Bonabeau *et al* (1996)

$$P_i(s_i) = \frac{s_i^2}{s_i^2 + \theta_i^2}$$

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[1] A thorough study of the effect of the level of variance in a population's response thresholds on rejection time was not carried out as part of this study, but is an obvious direction for further investigation.

where $P_i(s_i)$ is the probability of agent *i* attacking as a function of stimulus intensity , $s_i$ is the stimulus intensity of agent *i* and $\theta_i$ is the threshold of agent *i.* In the event that both agents attacked, the attacks were considered to have occurred simultaneously, and their health variables were updated after both attacks. Figure 2 illustrates several of the response curves that result from varying the threshold.

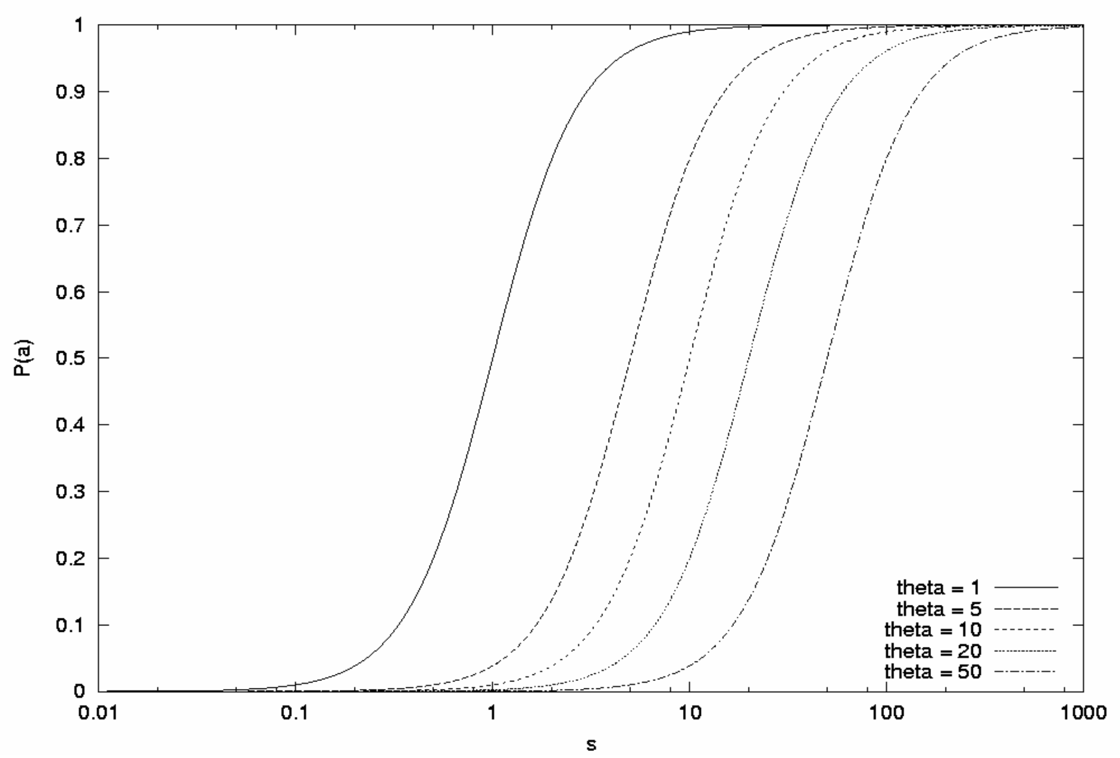

**Figure 2: Semi-log plot of the attack probability function for several different thresholds. When a termite has a high threshold, a low cue difference is likely to result in a low probability of attack. However, signals from low threshold members of the colony can raise the termite's stimulus to the point where an attack becomes more likely. Redrawn from Bonabeau, Théraulaz & Deneubourg (1996)**

Each simulation consisted of ten termites in the defending colony and one intruding termite. The parameters that were varied were cue difference, signal strength and response threshold. The data collected consisted of the time taken for the defending colony to eliminate the intruding termite. Each simulation was run ten times and the results were averaged.

The parameters in Table 1 were constant across all simulations. For the first set of simulations, the response threshold of the intruders and defenders was held constant and the cue difference and signal strength were systematically varied. For the second set of simulations, cue difference was fixed and the signal strength and response threshold were varied.

**Table 1: Constant Parameters**

| Parameter | Setting |
|---|---|
| Arena Size | 16 x 16 |
| Maximum Health | 2 |
| Signal Radius | 4 |
| Stimulus Decay | 0.1 |
| Number of Defenders | 10 |
| Number of Intruders | 1 |

Results:

In our model, social facilitation was found to decrease rejection time under two conditions – low cue difference and high response threshold. The results of the first set of simulations indicated that the importance of signaling decreased as the magnitude of the cue difference between the intruding and defending species increased (Figure 3). That is, when the intruding and defending species were closely related (low cue difference), social facilitation (strong signals) enabled an intruding termite to be rejected more rapidly. When the two species were less related (high cue difference), signaling was less important and rejection occurred rapidly anyway.

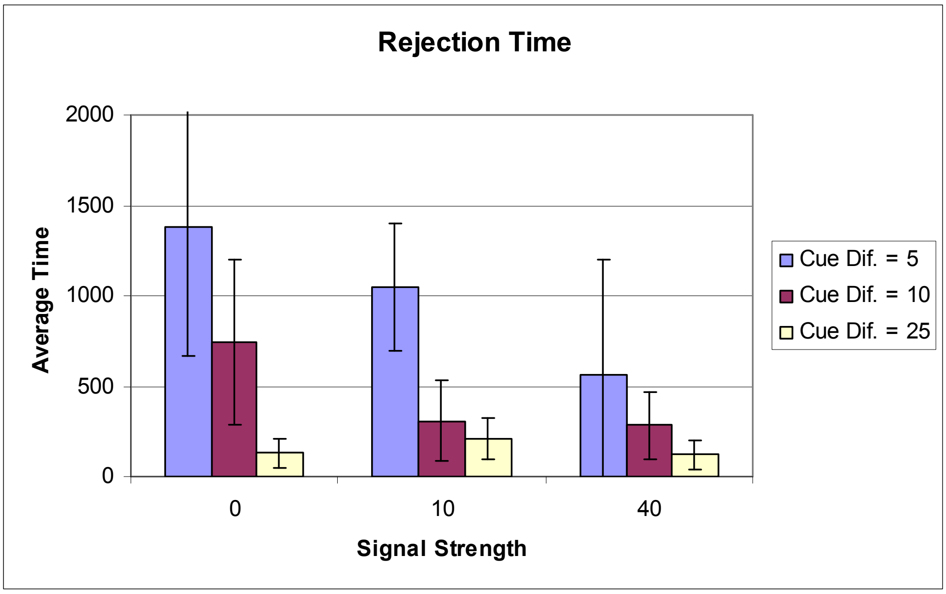

**Figure 3: The average time taken for a defending colony to reject an intruder when the cue difference between the colonies is low (5), medium (10) or high (25) and the signaling is absent (0), weak (10) or strong (40). When cue difference is high, signal strength does not have a significant impact on rejection time. When the cue difference is low however, signaling between individuals results in decreased rejection time.**

In the second set of simulations, signaling was observed to be more important when response thresholds were high (Figure 4). When the termites were less aggressive (high thresholds), stronger signaling enabled a more rapid rejection of the intruding termite. When the termites were more aggressive (low thresholds), rejection once again occurred rapidly, regardless of signaling strength.

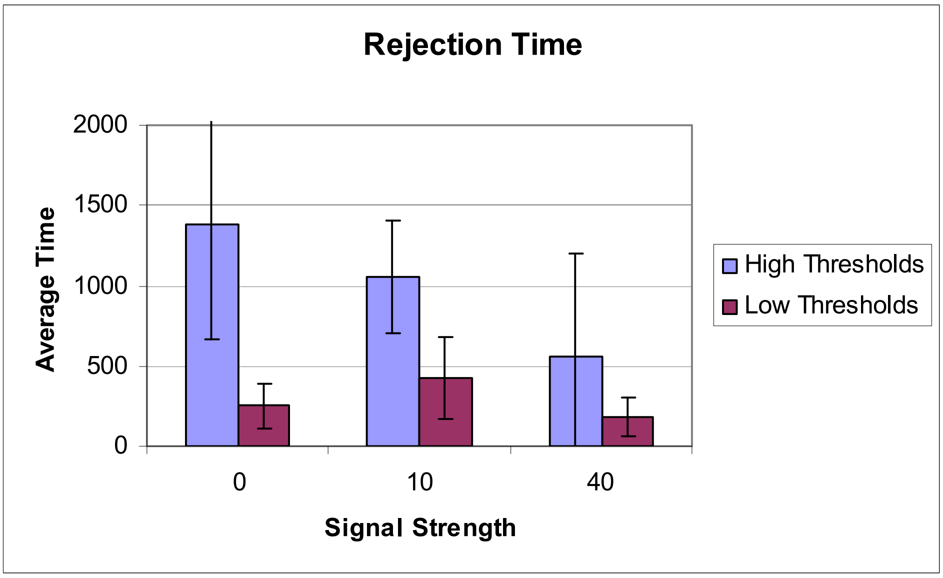

**Figure 4: The average time taken for a defending colony to reject an intruder when the cue difference between the colonies is low (5), signaling is absent (0), weak (10) or strong (40) and response thresholds are either high (30) or low (10). When response thresholds are low, signal strength does not have a significant impact on rejection time. When the response threshold is high, signaling between individuals results in decreased rejection time.**

## Discussion:

In the model developed for this study, we found that social facilitation had an impact on the expression of defensive behavior under several sets of conditions. When cue difference was low, increasing the amount of communication between individuals resulted in an observable decrease in rejection time that was not present when cue difference was high. Furthermore, when aggressiveness was low, communication also had a noticeable impact on rejection time that was not observed when aggressiveness was high.

The results from this model are analogous to laboratory results. When cue differences are large, they dictate the outcome of the interaction, regardless of signaling. This can be compared to interspecific aggression. In laboratory bioassays, rejection time for interspecific pairings occurs within 5 minutes, and always occurs more quickly than intraspecific pairings (Haverty *et al* 1999). Intraspecific pairings have considerably longer rejection times (Copren 2003, Haverty *et al* 1999). Therefore, lareg cue differences are analogous to interspecific interactions.

This simple model, therefore, provides a description of the possible mechanisms that influence recognition behavior. One model can account for the differences seen in interspecific and intraspecific recognition behavior, suggesting recognition acts along one pathway. It provides support that the lack of defensive behavior found in *R. flavipes* may be due to reduced genetic diversity between colonies. However, we cannot rule out the hypothesis that the species is simply less aggressive than other species that exhibit defensive behavior. Reduced aggression may be a function of ecological parameters. If resources are not scarce, and defense is costly, then aggressiveness may not be favorable. Therefore, *R. flavipes* may simply be a less aggressive species. Choosing between the two hypotheses requires a study comparing the genetic diversity of the two species. If *R. flavipes* is less genetically diverse, this provides support for the genetic diversity hypothesis.

This model supports the group effect seen in intraspecific interactions , likely due to social signaling. Without members of its colony, a single termite may not receive the required signals to lower its response threshold and to make accurate recognition decisions, particularly if its response threshold is already high. We can create another experiment to further strengthen the argument that signaling occurs. If social signaling occurs, then groups of workers where we simulate an attack before adding an intruder would have faster rejection times than groups of workers from the same colony that are not agitated. This is easily testable in the laboratory, and provides a logical experiment for further studies.

References Cited:

Adams, E S. (1991). Nest-mate recognition based on heritable odors in the termite Microcerotermes arboreus**.** *Proceedings of the National Academy of Sciences of the United States of America*, 88(5):2031-2034.

Beye, M., P. Neumann, M. Chapusiat, P. Pamilo, R.F.A. Moritz (1998). Nestmate recognition and the genetic relatedness of nests in the ant Formica pratensis. *Beh. Ecol. Sociobio*. 43 (1): 67-72.

Bonabeau, E., Dorigo, M. and Théraulaz, G. (1998). *Swarm Intelligence: From Natural to Articial Systems*. New York, NY: Oxford University Press.

Bonabeau, E., G. Théraulaz, J.-L. Deneubourg. (1997) Quantitative study of the fixed threshold model for the regulation of division of labour in insect societies. *Phil. Trans. Roy. Soc. London B* 268:1565-1569.

Boulay, R. & A. Lenoir (2001). Social isolation of mature workers affects nestmate recognition in the ant *Camponotus fellah*. *Beh. Processes* 55:67-73.

Breed, M.D. (1998) chemical cues in kin recognition: criteria for identification, experimental approaches and the honey bee as an example. In: Vander Meer, RK, Breed MD, Winston, ML, Espelie, K.E. (eds) *Pheromone communication in social insects:ants, wasps, bees, and termites*. Westview Press, Boulder, CO. pp 57-78.

Bulmer, M.S. and J.F.A. Traniello (2002). Lack of aggression and spatial association of colony members in *Reticulitermes flavipes*. *J. Insect Behav*. 15(1): 121-126.

Copren, K.A. (2003) Variation among colonies in defensive behavior may influence competitive ability. (in preparation)

Delphia, C.M., K.A. Copren, M.I. Haverty (2002) Agonistic behavior between individual worker termites from three cuticular hydrocarbon phenotypes of *Reticulitermes* (Isoptera:Rhinotermitidae) from Northern California . Ann. Entomol. Soc. Am. (submitted).

Fletcher, D.J.C, and C.D. Michener (eds.) (1987) *Kin Recognition in Animals*, John Wiley, New York.

Haverty, M.I., K.A. Copren, G.M. Getty, V.R. Lewis (1999) Agonistic behavior and cuticular hydrocarbon phenotypes of colonies of *Reticulitermes* (Isoptera:Rhinotermitidae) from Northern California. *Ann. Entomol. Soc. Am*. 92:269-277.

Haverty, M.I., & L.J. Nelson (1997) Cuticular hydrocarbons of *Reticulitermes* (Isoptera: Rhinotermitidae) from Northern California indicate undescribed species. *Comparative Biochemistry and Physiology B* 118 (4): 869-880.

Holway, D.A., A.V. Suarez, T.J. Case (1998) Loss of intraspecific aggression in the success of a widespread invasive social insect. Science (282):949-952.

Jenkins, T.M., Dean, R.E.; Verkerk, R.; Forschler, B. T. (2001) Phylogenetic analyses of two mitochondrial genes and one nuclear intron region illuminate European subterranean termite (Isoptera: Rhinotermitidae) gene flow, taxonomy, and introduction dynamics. *Molecular Phylogenetics and Evolution* 20(2): 286-293.

Kaib, M., S. Franke, W. Francke, R. Brandl (2002) Cuticular hydrocarbons in a termite: phenotype sand a neighbour-stranger effect. Phys. Entomol. 27:1-11.

Kirchner, Wolfgang H.; Broecker, Ingrid; Tautz, Juergen (1994) Vibrational alarm communication in the damp-wood termite *Zootermopsis nevadensis*. *Physiological Entomology* 19(3): 187-190.

Lacy, R.C. & P.W. Sherman (1983) Kin recognition by phenotype matching. *Am. Nat.* 121:489-512.

Lehman, L. & N. Perrin (2002) Altruism, dispersal, and phenotype-matching kin recognition. Am. Nat. 159:451-468.

Lenoir, A., D. Cuisset, A. Hefetz (2001) Effects of social isolation on hydrocarbon pattern and nestmate reacognition in the ant *Aphaenogaster senilis* (Hymenoptera:Formicidae). *Insectes Soc.* 48:101-109.

Marini, M. & B. Mantovani (2002) Molecular relationships among European samples of *Reticulitermes* (Isoptera:Rhinotermitidae). *Molecular Phylogenetics and Evolution* 22(3):454-459.

Matsuura, K. (2001) Nestmate recognition mediated by intestinal bacteria in a termite, *Reticulitermes speratus*. *Oikos* 92(1):20-26.

Miramontes, O. & DeSouza, O. (2002) The non-linear dynamics of survival and social facilitation in termites. Journal of Theoretical Biology (In press).

Page, M., L.J. Nelson, B.T. Forschler, M.I. Haverty (2002) Cuticular hydrocarbons suggest three lineages in *Reticulitermes* (Isoptera: Rhinotermitidae) from North America. *Comparative Biochemistry and Physiology Part B Biochemistry & Molecular Biology* 131B (3): 305-324.

Polizzi, J.M., and B.T. Forschler (1998) Intra- and interspecific agonism in Reticulitermes flavipes (Kollar) and R. virginicus (Banks) and effects of arena and group size in laboratory assays. *Insectes Soc*. 45:43-49.

Ruther, J., S. Sieben, B. Schricker (2002) Nestmate recognition in social wasps: manipulation of hydrocarbon profiles induces aggression in the European hornet. *Naturwissenschaften* 89:111-114.

Tsutsui, N.D., A.V. Suarez, D.A. Holway, T.J. Case (2000) Reduced genetic variation and the success of an invasive species. *Proceedings of the National Academy of Sciences of the United States of America* 97(11): 5948-5953.