

## Decision-making Systems in Recruitment to Food for two Nasutitermitinae (Isoptera: Termitidae)

by

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### ABSTRACT

Most termites exploit several different stable resources simultaneously using chemical mass recruitment systems to exploit new food sources. In the light of the decision-making system for recruitment (Democratic and Autocratic systems) described for ant species, this work studied the mass-recruitment system of the arboreal carton nest building termites *N. ephratae* and *N. corniger*. Our results show that these two species display recruiting dynamics that differ markedly from what was defined as “Democratic” decision making, conforming most closely to the ant’s “Autocratic” system, where scouts control the absolute amount of pheromone deposited on a trail according to the quantity and quality of the food source. These termites, however, seem to have additional features, making the regulation of the dynamics of the recruitment process much more complex than that described for ants. This work represents the first observations on the decision-making system used by termite societies in chemical mass recruitment to a new food source.

### INTRODUCTION

The mass recruitment system of ants has become a paradigm for computer scientists studying the dynamics of self-organization (Johnson 2000, for example). Yet, communication and decision making in real social insects are providing us with ever-new insights that surpass those obtained with pure imagination. For example, in termites that collect food at large distances from their nests, behaviours like exploration, trail building, and recruitment are collective processes that depend on finely regulated interactions between at least two castes which includes the presence of a caste that initiates the recruitment (Pasteels 1965; Oloo & Leuthold 1979; Traniello 1981; Oloo 1984; Kaib 1990; Lys & Leuthold 1991; Robson *et al.* 1995; Arab & Issa 2000; Fewell 2003, Chowdhury *et al.* 2004). Some of these behaviours such as recruitment with trails are modulated by chemical signals. The sternal gland has been recognized as a source of this trail pheromone

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in some termite species (Lüscher & Muller 1960; Stuart 1963), where two secretions have been found to be responsible for orientation and recruitment behaviour. These compounds are hexanoic acid, dodecatrienol, and neocembrene for Kalotermitidae and Termitidae (Moore 1966; Karlson *et al.* 1968; Tschinkel & Close 1973; Oloo & Leuthold 1979; Traniello 1981, 1982; Traniello & Busher 1985).

Regarding recruitment strategies, Wilson (1962) and Jaffé (1980) each presented a different model of decision-making that explained different strategies of chemical mass recruitment to food in ants. Both models were based on the following assumptions:

- 1) A recruitment process of workers can be induced and regulated with chemical signals alone,
- 2) The number of workers leaving the nest is controlled by the amount of trail substance deposited by foragers,
- 3) The trail pheromone orients the workers to the food source,
- 4) The more desirable the food find, the more trail pheromone is presented to the colony and hence, the more newcomer ants emerge from the nest,
- 5) The trail pheromone is a volatile substance, which if not reinforced on the trail, will evaporate below the threshold at a certain time, depending on the initial concentration of pheromone.

In this dynamic system, the pattern of trail reinforcement with pheromone by workers is determined by the decision-making system used during recruitment (Jaffé *et al.* 1985). This fact allows us to detect, by indirect methods, the decision making systems at work during a given recruitment process. Thus, we can experimentally confirm or not the several decision-making mechanisms that have been proposed to explain recruitment processes in terrestrial social insects. The model proposed by Wilson (1962) is the democratic alternative, where the information potential is uniformly distributed among the members in small bits, and the colony makes its decision by using information from the maximum number of colony members. That is, "the more desirable the food finds, the higher the percentage of ants laying pheromone trails." The model proposed by Jaffé (1992), described as an autocratic alternative, supposes that chemical recruitment to food sources may be initiated by a few scouts that provide the colony with all the information needed to decide the number of workers required at the food source. This means "that the number of newcomer ants that emerged from the nest is independent of the number of ants laying trails after inspecting the food". This is achieved thanks to a low response threshold towards the pheromone and a maximum concentration level on the trail, after which scouts add no more pheromone.

Table 1. Differences between the two decision-making systems

Features	Democratic	Autocratic	Reference
The number of individuals recruited depends on the number of trail-laying individuals returning to the nest	Yes	No	Jaffé <i>et al.</i> 1985
Trail pheromone concentration on the trail increases with the number of individuals returning to the nest	Yes	No	Jaffé <i>et al.</i> 1985
The number of workers recruited depends on the nest size (Nr of workers in the colony)	Yes	No	Verhaeghe & Deneubourg 1983
Castes specialized in initiating recruitment will improve food retrieval	No	Yes	Jaffé 1980, Jaffé <i>et al.</i> 1985
Number of simultaneous trials in one colony	Maximum one	More than one	Jaffé & Deneubourg 1993
Changes in the slope of recruitment curve with different food-nest distances	No	Yes	Sumpter & Beekman, 2003
Changes in the time to reach maximum recruitment with different food-nest distances	Gradual	Abrupt	Jaffé 1980, Jaffé <i>et al.</i> 1985
			Jaffé 1980

Table 1 summarizes the differences between these two recruitment systems. The first three points are evident from the description of both systems based on computer simulations (Jaffé 1980). The fourth point is a prediction based on the assumption that if only a few individuals are required to initiate recruitment, the possibility of workers specializing in this task in order to be more efficient is higher than if all individuals are involved in initiating recruitment (Jaffé *et al.* 1985). These features affect the recruitment kinetics, which in turn can reveal the decision-making system used by recruiting workers. Between the various features of the dynamics of the recruitment process that serve to reveal the underlying decision making system involved, the variation in recruitment dynamics at different food-nest distances showed to be the feature most sensitive to the decision making process and the easiest to measure (Jaffé *et al.* 1985).

By studying the relevant features of the recruitment kinetics in ants and by estimating various pheromone concentrations on the trail, Jaffé *et al.* (1985) showed

that both systems occur in nature.

Many termite species present chemical mass recruitment, but there is no information about the decision-making systems they use. The aim of this research is to work out the decision-making system used by the carton nest species *Nasutitermes corniger* and *N. ephratae* under laboratory conditions, by studying the relationships between the recruitment dynamics and the recruitment distance. The Termitidae

and especially the Nasutitermitinae are considered as the most socially specialized higher termites. These species have a large population on an arboreal nest and, at field and laboratory conditions, construct several galleries between the nest and the food source.

#### METHODS

Two arboreal nests of *N. corniger* (Motschulsky) and *N. ephratae* (Holmgren) were collected from areas of lowland forests at Barlovento, Miranda State (66° N, 11° W, 50 meters above sea level,  $T > 24^{\circ}\text{C}$  and precipitation between 600-1200 mm through the year), located in North-central Venezuela. Collections of nests were made from January to February 2000. The colonies to be collected were selected if no other conspicuous secondary nest were located near the colony, to increase the chances of collecting whole colonies. The carton nests were excised from host trees, placed in a plastic container, and taken to the laboratory at the Simon Bolivar University in Sartenejas, Miranda State, Venezuela. The colonies contained reproductive individuals, eggs, larvae, soldiers, and workers. The taxonomic identification was made using the nest architecture described by Thorne (1981) and the species *N. ephratae* were confirmed by DNA test made by Dr. Lynn Atkinson from James Cook University, Queensland, Australia.

We performed preliminary tests on food preference. The test consisted on placing different kinds of dry decayed wood (*Clusia* sp., *Erythrina* sp., *Acacia* sp. and *Piper* sp.), simultaneously on the plastic

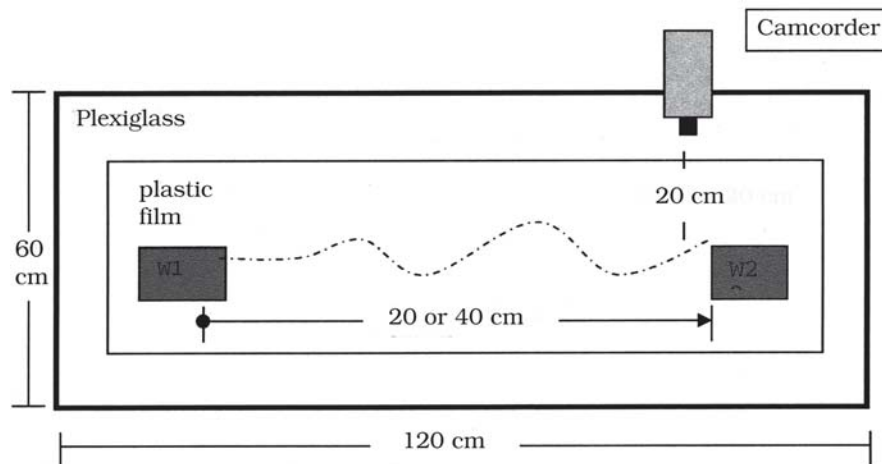


Fig. 1. Diagrammatic representation of the arena where the recruitment bioassays were made. The arrow shows the trail.

platform, next to the nest of both colonies from both species. We found that the most palatable wood was from *Erythrina* sp., the food that had the largest number of workers feeding on it among the others woods tested.

The nests were placed on a square plastic platform in an acclimatized room with 75-95% humidity and a temperature of  $25 \pm 5$  °C, the approximate conditions in the field. The photoperiod was set to 12:12 hours of light - darkness. Each nest was supplied with several pieces of moist dead wood (30-40 g of *Erythrina* sp.), a water source, and soil (20 g approximately) needed by worker for gallery construction. The experiments were conducted one week after the nests were brought to the laboratory.

To find out which recruitment system is used by each species, we performed the following bioassay. Over a white Plexiglas platform, (60 x 120 cm) we placed a transparent plastic sheet (40 x 60 cm). This sheet was changed for a new one before each assay. On one extreme (see Fig. 1), we placed a piece of wood. Wood 1 (W1) was taken from the pieces previously placed near the nest, containing about 1.500-2.500 termites including soldiers and workers. Wood 2 (W2) was a new piece of dead wood without termites (about 35-40 g of *Erythrina* sp.). Each W2 was dried in a stove for 24 hours at 60° C.

Distances were chosen based on preliminary tests, so that initiation of recruitment would take less than one-hour. The chosen distances were 20 and 40 cm for both species. For each distance chosen, 10 replicate experiments were made. At the time when both wood pieces were placed over the plexiglas platform, we began to film the individuals engaged in exploration and recruitment between W1 and W2. This was filmed using a Sony handy cam (CCD-TRV37) during nighttime using the night shot light mode. The lens was focused over W2 (Fig. 1). The distance between the Handy Cam and W2 was 20 cm. After each test, W2 was removed, and the termites present were weighed to estimate the number of individuals.

Each video was reviewed to count the number of individuals from each caste arriving at W2. We measured several variables:

1. The initial time of recruitment was the moment the first individual arrived at W2. Then we made observations for 1 min every 5 min for 3 hours.

2. The time of maximal recruitment activity was the time between the initial time and the moment when the maximum number of foragers was counted at W2.

3. The total number of individuals was calculated at the end of the bioassays counting the number of individual's presents at W1 and W2.

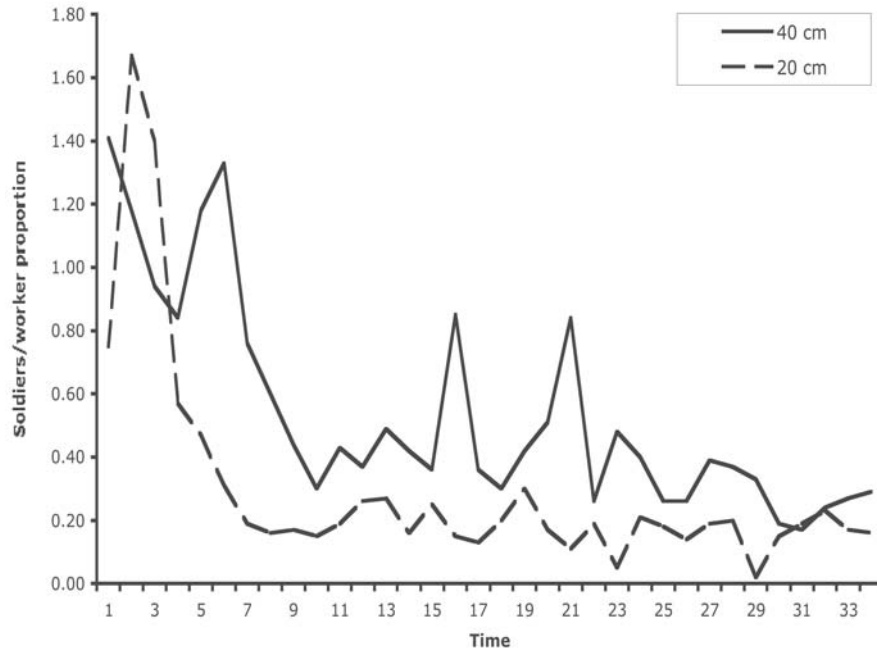


Fig. 2. Average of soldier/workers proportions of *N. ephratae* recruitment to a new food for two distances (10 replicates for each distance).

4. The slope of the rapid recruitment phase was calculated with a linear regression model fitted to a regression coefficient ( $R^2$ ), on the rapid increase phase of the recruitment curve. This curve was determined graphically for each replicate experiment, plotting the number of individuals going to W2 vs. the interval time they took to make it (Jaffé 1980, Jaffé *et al.* 1985). A Mann-Whitney test was used to determine differences between the values of the variables from replicates for each of the two distances for each species.

## RESULTS

*N. corniger* and *N. ephratae* have a similar behavior in the presence of a new food source. The behavior observed could be described as follows: most commonly, we found that soldiers (2 or 6 individuals) were the first to initiate the exploration towards the new food source. Regarding the behavior at the food source, we observed that the scouts remained at the food for 5 to 15 minutes. After this time they returned to the nest, abdomen pressed to the substrate, chemically marking the initial exploratory trail (Arab *et al.* unpublished data) between W1 and W2. This started the recruitment phase. Workers, when contacting the

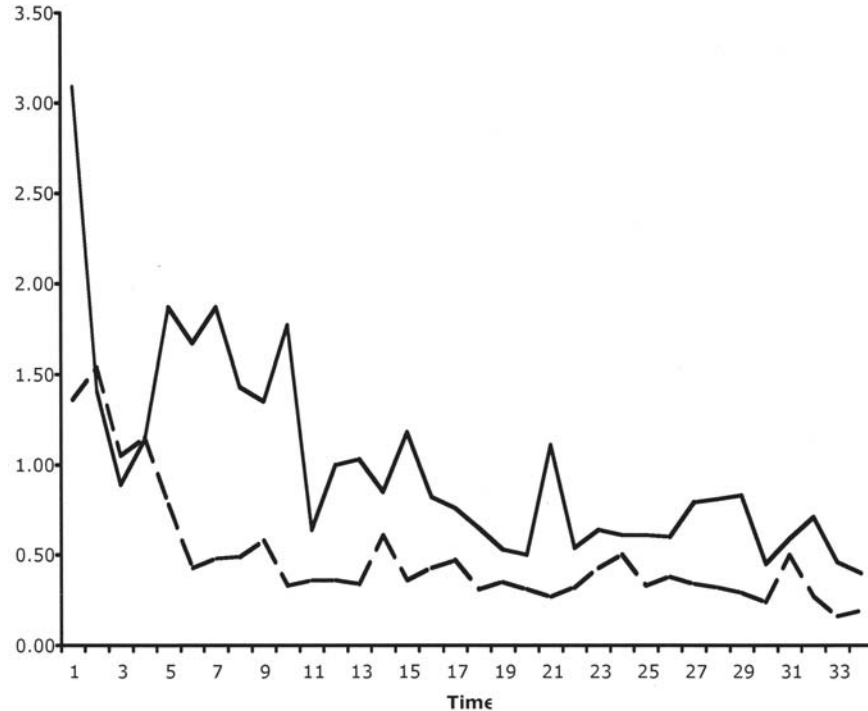


Fig. 3. Average of soldier/workers proportions of *N. corniger* recruitment to a new food for two distances (10 replicates for each distance).

trail started following it to the food source. After some time, increasing number of workers arrived at the food source. The number of workers recruited to the food source stabilized and then decreased. Eventually the termites would build a covered gallery leading from the nest to the food. Soldiers remained on the trail, but the proportion soldier/worker on the trail decreases after a few minutes. This behavior was found for both species at the distances studied (Figs. 2 and 3).

Table 2 shows the time when the largest number of individuals was recruited, at the end of the rapid recruitment phase, for the two distances studied. Data for both, *N. ephratae* and *N. corniger*, showed that the maximum number of foragers was reached first at the shorter distance compared to the larger recruitment distances. This difference was statistically significant.

The average  $\pm$  standard error (SE) of the total number of individuals participating in the recruitment processes of the various bioassays was  $2620.9 \pm 382.9$  for *N. ephratae* and  $1938.7 \pm 228.5$  for *N. corniger*. This number was statistically indistinguishable between the bioassays with

Table 2. Mean and standard deviation of the time of maximal recruitment activity for *N. ephratae* and *N. corniger* at two different food-nest distances.

Distance (cm)	Time (min)			
	<i>N. ephratae</i>	N	<i>N. corniger</i>	N
20	39.5 ± 10.5	10	43.0 ± 10.5	10
40	50.5 ± 9	10	63.5 ± 16	10

Mann-Whitney's test comparing the two distances			
U	18		13
Z	2.42		2.62
p	0.016		0.009

different foraging distances. The total number of termites participating in the recruitment process represented a small proportion ( $\pm 0.67\%$ ) of the total estimated number of termites in the nest. The experiments studying the slope of the recruitment curve are illustrated in Figs. 4 and 5. The slopes of the curves are very similar, with no statistically significant differences among them for the two distances studied (Table

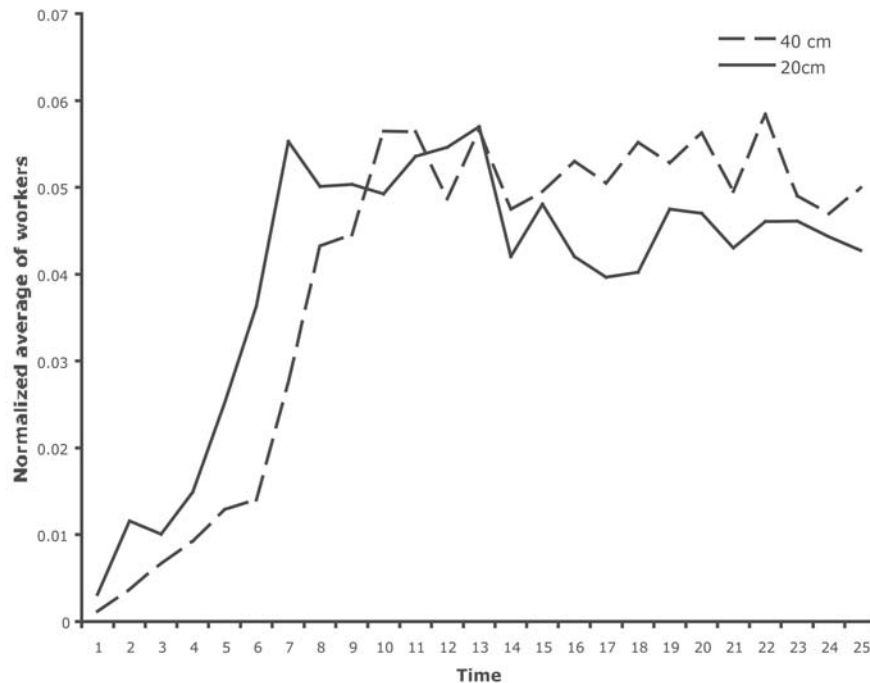


Fig. 4. Food recruitment curves, under laboratory conditions, of workers of *N. corniger* for two distances (10 replicates for each distance).

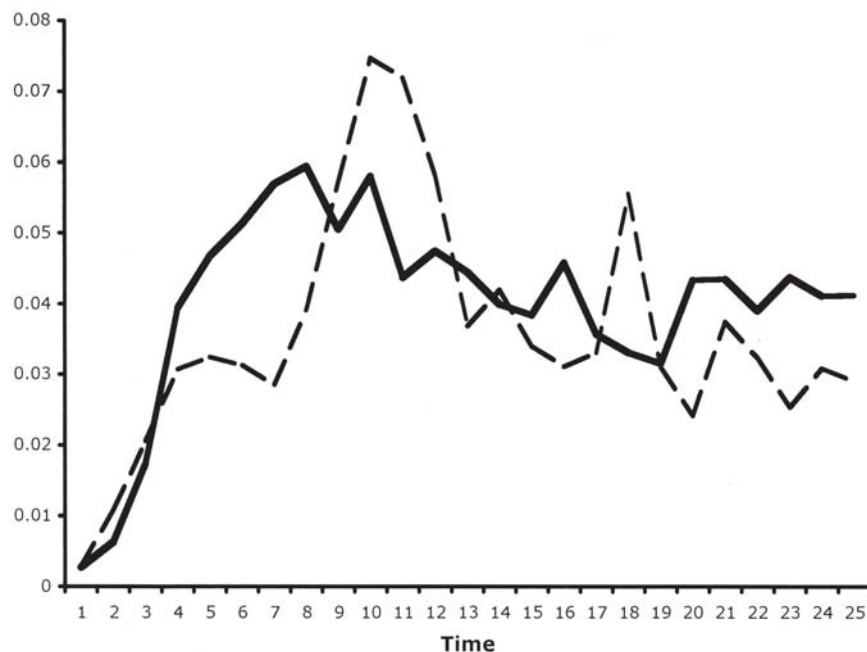


Fig. 5 Food recruitment curves, under laboratory conditions, of workers of *N. ephratae* for two distances (10 replicates for each distance).

Table 3. Slope of the recruitment curve (Normalized Mean  $\pm$  SD) for *N. ephratae* and *N. corniger* at two different food-nest distances.

Distance (cm)	Slope (individuals/min/total individual number)			
	<i>N. ephratae</i>	N	<i>N. corniger</i>	N
20	0.046 $\pm$ 0.031	10	0.038 $\pm$ 0.031	10
40	0.048 $\pm$ 0.034	10	0.044 $\pm$ 0.032	10

Mann-Whitney's test comparing the two distances			
U	47	39	
Z	0.23	0.49	
P	0.82	0.62	

3). That is, the slopes of the recruitment curves do not decrease with increasing distance to food, despite the fact that our method could detect longer periods for reaching maximum recruitment at the larger distance (Table 2).

We found an interesting behaviour where, from the same initial wood block (W1), two different trails went to the new source. For *N. corniger*, seven of 10 bioassays (for both distances) had two different trails to W2.

This behaviour was found, also on *N. ephratae*, where 3 of 10 bioassays at the distance of 40 cm, and 4 of 10 when the distance was 20 cm present 2 different trails, simultaneously. This behaviour was similar to that found in the field for both species. Often, these arboreal nests have two or more conspicuously active trails with termites foraging at the same time (personal observations).

#### DISCUSSION

Regarding the behaviour when a few scouts look for a new food source was found by Arab & Issa (2000) for the same species, Miura & Matsumoto (1998) for *Hospitalitermes rufus* and *H. medioflavus*; Traniello & Busher (1985) for *N. costalis*; and Collins (1979) for *H. umbrinus*.

Taken together, our results showed that:

1. Specific castes (soldiers or "scouts") initiate the recruitment curve.
2. Recruitment distance does not affect the slopes of the recruitment curve, but affect the time maximum recruitment activity is reached.
3. These termites normally forage simultaneously on various large, semi-permanent, food sources in the field.
4. Termites use more than one trail to forage to a given food source in the laboratory.

These results suggest that the recruitment behaviour of these termites have similar features of those described for the autocratic system found for Attini ants (Jaffé *et al.* 1985). In a democratic system one expects to see a decrease in the slope of the recruitment curve at larger recruitment distances, and the times to reach maximum recruitment are gradual (Table 1). The fact that more than one trail may lead to a single food source is very important. The dynamics of chemical recruitment using a democratic decision making system does not allow for two or more trails to coexist (for example see Beckers *et al.* 1990, Johnson 2000, Sumpter & Beekman 2003). As workers will inevitably be attracted to the trail with the most pheromone concentration, soon the second trail will be less attractive because the pheromone on the way in will not reinforce, therefore all workers will be using the most active trail.

The fact that the species studied showed an autocratic recruitment system and that they forage on food sources predictable in time and space is consistent with the predictions of Jaffé & Deneubourg (1992). However, recruitment systems in termites are much more complex than in ants, as soldiers and workers have quite different roles and behaviour during recruitment (Arab 1998, Arab & Issa 2000), as could be also confirmed with our observations.

One major difference between recruitment studies in ants and the study reported here for termites is the definition of food-nest distance. While for ants the distance is unambiguously defined (from the nest opening to the food source), for the termites, conspicuous nests do not have a principal opening. The distance to the food is then defined as the stretch from an active trail to the food. This definition involves the difficulty of assessing the activity of the trail chosen. This problem is very clearly reflected in the variability of the replicas regarding the time for the initiation of the rapid recruitment phase. Figures 4 and 5 though show that despite the large variability in the time termites take to initiate recruitment, the slopes of the recruitment curves are very constant, an important characteristic of the autocratic decision making system.

Thus, the cumulative evidence suggests that both *Nasutitermes* species employ an autocratic decision system during chemical mass recruitment to food, in which a few individuals (mostly soldiers) provide all (or most of) the information needed for the initiation of the recruitment process. The results of this work represent the first observations of the decision making-system used by termite societies in chemical mass recruitment to new food sources. These processes could well be much more sophisticated in termites than what has been described for ants. It would be interesting to determine whether the decision-making systems differ among less evolved termite groups.

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#### REFERENCES

- Arab, A. 1998. Comportamiento de seguir trillas de dos especies de termitas arbóreas (Isoptera: Termitidae: Nasutermitinae). Thesis, Licenciatura en Biología, Universidad Simón Bolívar. Venezuela 50 pp.
- Arab, A. & S. Issa 2000. Breves observaciones sobre el comportamiento de forrajeo de dos especies de termitas (Termitidae: Nasutitermitinae) bajo condiciones de laboratorio. Boletín de Entomología Venezolana 15: 93-95.
- Beckers, R., J.L. Deneubourg, S. Goss & J.M. Pasteels 1990. Collective decision making through food recruitment. *Insectes Sociaux* 37: 258-267
- Chowdhury, D., K. Nishinari & A. Schadschneider 2004. Self-organized patterns and track flow in colonies of organisms: from bacteria and social insects to vertebrates. arXiv:q-bio.PE/0401006 v2
- Collins, N. 1979. Observations on the foraging activity of *Hospitalitermes umbrinus* (Havilland) in the Gunong Mulu National Park, Sarawak. *Ecological Entomology* 14: 231-238.

- Fewell J.H. **Need year** Social Insect Networks. *Science* 301: 1867-1870.
- Jaffé, K. & J. L. Deneubourg 1992. On foraging, recruitment systems, and optimum number of scouts in eusocial colonies. *Insectes Sociaux* 39: 201-213.
- Jaffé, K., G. Villegas, O. Colmenares, H. Puche, N. Zabala, M. Alvarez, J. Navarro & E. Pino 1985. Two different decision-making systems in recruitment to food in ant societies. *Behavior* 92: 9-21.
- Jaffé, K. 1980. A theoretical analysis of the communication system for chemical mass recruitment in ants. *Journal of Theoretical Biology* 84: 589-609.
- Johnson, N.L. 2000. Developmental Insights into Evolving Systems: Roles of Diversity, Non-Selection, Self-Organization, Symbiosis. *Artificial Life VII*. Cambridge Mass. MIT Press.
- Kaib, M. 1990. Intra- and interspecific chemical signals in the termite *Schedorhinotermes* – production sites, chemistry, and behavior. *In: Sensory systems and communications in arthropods* (F. Gribahin, K. Wiese, and A. Popov, Eds.), pp. 26-31. Basel: Advances in life sciences.
- Karlson, P., M. Lüscher, & H. Hummel 1968. Extraktion und biologische Auswertung des Spunpheromones der Termiten *Zootermopsis nevadensis*. *Journal of Insect Physiology* 14: 1763-1771.
- Lüscher, M. & B. Müller 1960. Ein spurbildendes Sekret bei Termiten. *Naturwissenschaften* 21: 503.
- Lys, J. & R. Leuthold 1991. Task-specific distribution of two worker caste in extranidal activities in *Macrotermes bellicosus* (Smeathman): observation of behavior during food acquisition. *Insectes Sociaux* 38: 161-170.
- Miura, T. & T. Matsumoto 1998. Foraging organization of the open-air professional lichen – feeding termite *Hospitalitermes* (Isoptera, Termitidae) in Borneo. *Insectes Sociaux* 45: 17-32.
- Moore, B. P. 1966. Isolation of the scent-trail pheromone of an Australian termite. *Nature* 211: 746-747.
- Oloo, G. & R. Leuthold 1979. The influence of food on trail-laying and recruitment behavior in *Trinervitermes bettonianus* (Termitidae: Nasutitermitinae). *Entomologia Experimentalis et Applicata* 26: 267-278.
- Oloo, G. 1984. Some observations on the trail-laying behaviour of *Macrotermes michaelseni* (Sjost) (Termitidae). *Insect Science Applied*. 5:259-262.
- Pasteels, J. 1965. Polyethime chez les ouvrières de *Nasutitermes lujae* (Termitidae: Isopteres) *Biologia Gabonica*. 1: 191-205.
- Robson, S.K., M.G. Lesniak, R.V. Kothandapani & J.F.A. Traniello 1995. Non-random search geometry in subterranean termites. *Naturwissenschaften*. 82: 526-528.
- Stuart, A. M. 1963. Origin of the trail in the termites *Nasutitermes corniger* (Motschulsky) and *Zootermopsis nevadensis* (Hagen), Isoptera. *Physiological Zoology* 26: 69-84.
- Sumpter, D.J.Y. & M. Beekman 2003. From nonlinearity to optimality: pheromone trail foraging by ants. *Animal Behaviour* 66: 273-280
- Thorne, B. 1981. Differences in nest architecture between the Neotropical arboreal termites *N. corniger* and *N. ephratae* (Isoptera: Termitidae). *Psyche* 87: 223-243

- Traniello, J. 1982. Recruitment and orientation components in a termite trail pheromone. *Naturwissenschaften* 69: 343-344.
- Traniello, J. 1981. Enemy deterrence in recruitment strategy of Soldiers-organized foraging in *Nasutitermes costalis*. *Proceedings of the Natural Academic of Science* 78: 1976-1979.
- Traniello, J. & C. Busher 1985. Chemical regulation of polyethism during foraging in Neotropical termite *Nasutitermes costalis*. *Journal of Chemical Ecology* 11: 319-332.
- Tschinkel, W. & P. Close 1973. The trail pheromone of the termite *Trinervitermes trinervoides*. *Journal of Insect Physiology* 19: 707-721.
- Verhaeghe, J. C. & J. L. Deneubourg 1983. Experimental study and modeling of food recruitment in the ant *Tetramorium impurum* (Hymenoptera: Formicidae). *Insectes Sociaux* 30: 347-360
- Wilson, E. O. 1962. Chemical communication among workers of the fire ant *Solenopsis saevissima*. *Animal Behaviour* 10: 134-164.



