Intraspecific Interactions in a Community of Arboreal Nesting Termites (Isoptera: Termitidae)

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In coconut plantations of northern New Guinea, the arboreal nesting termite community comprises three species: Nasutitermes princeps, N. novarumhebri-darum, *and* Microcerotermes biroi. *In order to assess the importance of intra-specific interactions in this community, we conducted pairwise encounters between batches of individuals in the laboratory and between entire nest populations in seminatural conditions. Three levels of agonism were defined in laboratory bioassays: anagonism, moderate agonism, and strong agonism. Anagonism was observed during all control tests with homocolonial groups and in some tests with allocolonial groups of all species. Moderate agonism included initial aggressiveness that subsequently faded out, and initially passive encounters where aggression progressively built up and led to fighting. Strong agonism corresponded to initial aggressiveness and fighting. Results obtained in laboratory bioassays were consistent with bioassays in seminatural conditions. When* Nasutitermes *colonies were anagonists in laboratory bioassays, their foraging trails merged without aggression in field tests. N.* princeps *nests that were moderately agonistic in laboratory tests fought and either continued to avoid each other or finally joined after elimination of the most aggressive individuals. The most aggressive M.* biroi *and N.* princeps *colonies fought and their foraging trails diverged afterward. Direct attacks on alien nests were witnessed in M.* biroi. *In all species, anagonism occurred in 21–34% of the combinations tested, between either geographically close or distant colonies. An exception was a group of 112 anagonist nests of N.* princeps, *which most probably constituted a supercolony. The level of agonism between* Nasutitermes *colonies was constant during the wet and dry season. Termite colonies excluded each other, both intra- and interspecifically, from the coconut trees, and their territories seem distributed in a mosaic pattern. Agonism between colonies may result in the elimination of the weakest colonies or in trail divergence, maintaining this*

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mosaic. In contrast, lack of agonism between some colonies suggests the possibility of colony fusion and gene exchanges without nuptial flights.

INTRODUCTION

Termite colonies are generally closed to allocolonial conspecifics (reviewed by Thorne and Haverty, 1991). Some species maintain territories from which intruders are apparently excluded. Aggressive interactions at the territory boundary of conspecific colonies have been evidenced in the mound-building termite *Macrotermes michaelseni* (Darlington, 1982), in the subterranean termite *Heterotermes aureus* (Jones, 1993), and in the arboreal nesting termite *Nasutitermes nigriceps* (Levings and Adams, 1984). Such intraspecific aggressiveness, often together with interspecific antagonism, apparently affects the spatial distribution of colonies: mounds in African and Australian ecosystems are often overdispersed (Wood and Lee, 1971; Collins, 1981; Lepage, 1984; Abe and Darlington, 1985; Spain et al., 1986; Pomeroy, 1989), and territories of *Heterotermes aureus* (Jones and Trosset, 1991; Jones, 1993) and of *Nasutitermes* spp. (Levings and Adams, 1984; Adams and Levings, 1987) apparently form a mosaic similar to mosaics of territories of dominant ants (review of Majer, 1993; Adams, 1994). In contrast, conspecific colonies may also fuse, as observed in *Coptotermes formosanus* by Su and Scheffrahn (1988).

In coconut plantations of the northern New Guinea coastline, the arboreal nesting termite community comprises three species of Termitidae which exclude each other from coconut trees, offering special interest for studies on competition. On average, 1 ha of a dense coconut plantation supports 234 trees, 100 of which are occupied by 28 *Microcerotermes biroi* colonies, 21 by 3 *Nasutitermes princeps* colonies, and 6 by 2 *N. novarumhebridarum* colonies (Leponce et al., 1995, 1996a). In a previous study, we provided evidence for asymmetries between competitive abilities in the three species: both *Nasutitermes* were able to destroy *M. biroi* colonies; this ability allowed *N. princeps* to expand its colonies in a habitat preempted by the faster colonizer, *M. biroi* (Leponce et al., 1996a,b). *N. novarumhebridarum*, which apparently prefers dead trees (Roisin and Pasteels, 1987; Leponce et al., 1995), has more restricted colonies and interferes less with the two other species. Until now, intraspecific relationships have received little attention except in *N. princeps*, where the existence of agonism between neighbor colonies was previously demonstrated, although lack of agonism sometimes occurred between individuals from different colonies (Roisin et al., 1987). Interactions between *M. biroi* colonies are probably fre-

quent because of the high density of colonies in this habitat and also in *N. princeps* since large concentrations of nests are sometimes found. In *N. novarumhebridarum*, allocolonial individuals may also encounter, especially on dead trees.

The goals of the present study were to assess the frequency and intensity of intraspecific agonistic interactions between colonies of the three species and to evaluate factors possibly affecting aggressiveness in order to estimate the influence of intraspecific agonism on community structure. To reach these goals, we performed laboratory bioassays between groups of individuals from different colonies (or from the same colony as controls) of each of the three species. Because it is still uncertain whether laboratory bioassays, conducted under highly artificial conditions, are representative of natural encounters (Thorne and Haverty, 1991), we corroborated and extended the laboratory tests by confronting entire nests on an experimental area in seminatural conditions. Individuals from the same pairs of nests were confronted in different seasons because a seasonal variation of agonism has been observed in European *Reticulitermes* species (Clément, 1986). Agonism among close neighbors (nests from the same site) and nests from distant sites was compared, as the latter are less likely to be genetically closely related and as it has been demonstrated that genetic relatedness affects to some extent allocolonial aggressiveness in another arboreal termite, *Microcerotermes arboreus* (Adams, 1991).

MATERIALS AND METHODS

Study Sites

Colonies tested came from coconut plantations spread along a 30-km coastal strip from Bogia to Awar, Madang Province, Papua New Guinea.

Aggression Bioassays in the Laboratory

Termites used in laboratory bioassays were collected by removing a portion of their nest in the field. In all species, pairwise bioassays between neighbors (colonies from a single site) and between nonneighbors (colonies from different sites) were carried out. As controls, trials were also conducted between termites coming from the same colony. Twenty-six nests of *N. princeps* from 4 sites, 18 nests of *N. novarumhebridarum* from 4 sites, and 15 nests of *M. biroi* from 5 sites were used in these tests. The experimental groups were composed of soldiers and large workers (at a soldiers:workers ratio of 3:17 in *M. biroi* and 1:1 in *N. princeps* and *N. novarumhebridarum*, in order to simulate foraging groups) and placed in plastic petri dishes 5.5 cm in diameter lined with moist filter paper. Three tests per combination were performed: two replicates in a

one-dish arena and one replicate in a three-dish arena. Preliminary and a pos-
teriori comparisons of the two experimental setups indicated that they yielded
the same results. More replicates were performed when dubious results were
obtained and some tests were replicated over time (see below). In the one-dish
setup, a group of 20 individuals on a nest fragment from one colony (A in Fig.
1a) was placed into a petri dish, then confronted with a group of 20 individuals
from another colony (B in Fig. 1a) holding to a nest fragment. The three-dish
arena was a refined version of the one-dish arena: the number of termites per
colony was doubled and the confrontation method was less disruptive. The
experimental arena was composed of three petri dishes glued together in a straight
line and communicating by holes 4 mm in diameter (Fig. 1b). During the accli-
matization period, both termite groups were confined in their own petri dish by
a plastic cylinder (as in dish containing A, Fig. 1b). At the beginning of the
test, these cylinders were removed and the arena covered with a glass slide.
Behaviors during encounters were then video recorded under low light (260 lux)
for 3 to 30 min. The videotapes were reviewed later and allowed more detailed
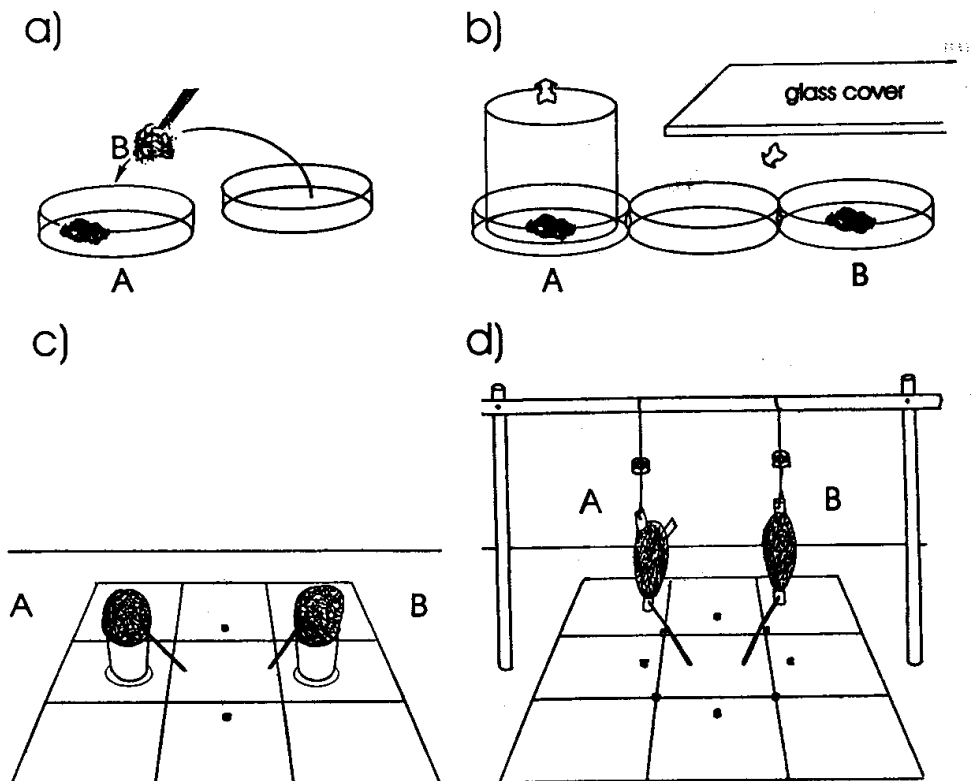observations of agonistic reactions. A dot of yellow paint on the abdomen dis-

Fig. 1. Experimental setups used in laboratory and field bioassays: (a) single-petri dish
arena; (b) three-petri dish arena; (c) experimental area used to confront the population
of two *Nasutitermes* spp. nests placed in plastic containers; (d) portico used to confront
the population of two *M. biroi* nests hung by ropes and connected to the experimental
area with two sticks. For details see text.

tinguished members of one colony from the other. The paint (ICI Dulux exterior gloss acrylic) was water based and dried within 20 min at 25°C; our preliminary laboratory tests indicated that it caused no observable mortality or behavioral modification. All assays were performed on the day termites were collected to avoid any effect of prolonged isolation of termites from their home colony and were initiated when termites were quiet and gathered on the fragment of their nest material, generally within less than 3 h after introduction of the termites. Any manifestation of aggressiveness or lack thereof was noted during the 3 min following the first encounter between allocolonial termites. Five levels of initial aggressiveness were recognized: (1) indifference—no examination, walking at normal speed, forward-and-backward body oscillation; (2) discrimination—prolonged unilateral or mutual antennation, pursuit; (3) threats, nip—bites inflicting no apparent injury; (4) strong alert—jerk back when in contact with alien, increase in locomotory speed, frenetic forward-and-back oscillation; and (5) attack—bites that pierce the exoskeleton, emission of defensive secretion (*Nasutitermes* soldiers only), head banging (*M. biroi* soldiers only). Dead or conspicuously wounded workers and soldiers were counted after 24 h. Initial aggressiveness and final mortality were combined to define a level of agonism between the two colonies. Level I, anagonism, and level III, strong agonism, are opposite responses. In level I, no initial aggressiveness was observed; death rate, never due to fighting, was below 10%. In level III, initial aggressiveness (threats, strong alert and attack) or at least evident discrimination always was observed and death rates, due to fighting, were always over 10%. Level II, moderate agonism, covers all intermediate outcomes, i.e., no initial aggressiveness but high delayed mortality or initial aggressiveness but low mortality (< 10%) and even, in some of the replicates, no evidence of agonistic reactions and of mortality due to fighting. When moderate agonism was detected, additional replicates (up to 15, depending on the availability of material) were generally performed.

Assays involving *N. princeps* and *N. novarumhebridarum* were first conducted in July–August 1991, during the dry season, and repeated during the wet season in February–March 1992. Assays involving *M. biroi* were conducted only during the wet season, in April–May 1992. Additional tests were performed in 1993 and 1994 in order to compare results yielded in the laboratory and in seminatural conditions (see below).

Aggression Bioassays with Entire Nests in Seminatural Conditions

To force encounters between termite colonies, nests were transplanted from the field to experimental areas of 9 m² of cleared ground. A grid of ropes 1 m apart facilitated mapping of foraging trails. Nine of these areas were established on Laing Island in the forest near King Léopold III Biological Station. The experimental setup was inspired by that used by Thorne (1982a) but was adapted

to the nest volumes of the studied species. Experiments involving *N. princeps*, *M. biroi*, and *N. novarumhebridarum* colonies were conducted in, respectively, May–June 1993, June–July 1993, and April 1994. Colonies were confronted for at least 4 days and up to 3 weeks. A sample of the nests' population was collected prior to test initiation and at the end of the experimental period.

Entire *Nasutitermes* nests with a volume ranging from 60 to 100 liters were collected in the field by removing them from the tree trunk and placing them directly in a large plastic container (garbage bin), which was then brought to Laing Island. Containers were arranged on the experimental area, which comprised two wood baits 1.4 m apart (Fig. 1c). Each container, from which termites could not escape, contained a small amount of dead wood and moist paper. Ants were prevented from entering the nest by a water barrier. Two days of acclimatization allowed the termites to rebuild some parts of their nest and allowed time to assess agonism between colonies in laboratory bioassays conducted as described above. After the acclimatization period, a stick was positioned to connect each nest with the ground so that they were 80 cm apart. Some individuals from each colonies were marked with yellow and red Magix color spray. We tested the outcome of encounters among foragers of nests which appeared to be anagonists, moderate agonists, and strong agonists in laboratory bioassays. We focused on *N. princeps* (10 nests paired) because this species is more common in plantations than *N. novarumhebridarum* (2 anagonist nests paired).

Small trees supporting *M. biroi* nests were cut in a secondary forest and brought to Laing Island. The volume of collected nests ranged between 13 and 35 liters. On Laing Island, nests were hung with a rope to a portico (Fig. 1d). Eight baits composed of small pieces of wood were arranged along a circle (radius, 70 cm) at the center of the setup. A barrier of water around the rope prevented escapes of termites and attacks by ants during a 2-day acclimatization period during which laboratory bioassays were conducted. Sticks were then installed to connect the nests to the ground. Sticks at a distance of 15 cm in two initial tests were placed 50 cm apart in the following tests because 15 cm did not provide enough opportunity for termites from the two nests to avoid each other. We did not succeed in finding anagonist *M. biroi* nests in the forest for these experiments.

RESULTS

Agonism Between *N. princeps* Colonies

Aggressive Behaviors

In anagonistic encounters (level I), groups of termites from two nests behaved as in controls: during the first encounters, they showed some excitement

by displaying oscillatory movements that dissipated rapidly as the two groups mixed together. The death rate of groups of soldiers and workers in anagonistic encounters was 0.02 ± 0.02 (average $\pm$ SD; $n = 210$) (Fig. 2a), which was not significantly different from that of controls, 0.02 ± 0.02 ($n = 160$; $t = 0.81$, df $= 368$, $P = 0.421$). In moderately agonistic encounters (level II), some *N. princeps* individuals reacted to the presence of aliens, while others did not. Discriminatory behaviors never arose without contact with an alien. Aliens were sometimes examined for a prolonged period (for more than 10 s). After discrimination, three levels of increasing aggressiveness could be reached: (i) nipping or avoidance; (ii) alarm—termites jerked back when they touched an alien and displayed an increased walking speed or a faster oscillatory movement; and (iii) attack, i.e., bites by workers, causing severe wounds, or projection of defensive secretion by nasute soldiers. A wide range of aggressive responses was observed in bioassays with moderately agonistic colonies: in some cases, a few termites were very aggressive and the others apparently indifferent; in other cases, most of the termites displayed mild agonistic behavior. Video recordings showed that aggressiveness was sometimes high but delayed for up to 10 min after initial contact. The death rate in moderately agonistic encounters was variable (0.36 ± 0.34; $n = 132$) and bimodally distributed (Fig. 2a): in some bioassays, individuals showing initial aggressiveness either calmed down or were killed in fights without eliciting further aggression, and mortality was low; in other tests, alarm and aggression, though initially low or restricted to a few individuals, propagated until generalized fighting erupted, and the resulting mortality was high. Very variable responses were sometimes observed among replicates involving the same colonies. For example, between moderately agonistic nests laboratory bioassays revealed the following results: nest V versus nest VI—four replicates with neither initial aggressiveness nor a high final mortality, two replicates with initial aggressiveness but no mortality, eight replicates with initial aggressiveness and a high final mortality, and one replicate without initial aggressiveness but with high final mortality due to fighting; for nests VII and VIII the number of replicates falling in each category was, respectively, 5, 4, 6, and 0. In strongly agonistic encounters, a large number of *N. princeps* were aggressive after a short period of contact with aliens and the resulting mortality was invariably high (0.74 ± 0.13; $n = 87$) (Fig. 2a).

Frequency of Agonism in Laboratory Bioassays

N. princeps colonies coming from four sites were confronted in laboratory bioassays during two consecutive seasons (Fig. 3). Site A2 was unique for its abundance of *N. princeps:* 112 nests were recorded on 3.1 ha in 1991. The map presented in Fig. 3 shows a portion of this site where 86 nests were present. No agonism was detected in any of the 40 combinations tested between the 15 largest nests (Fig. 3). Ten of these nests were opened and all were polygynous,
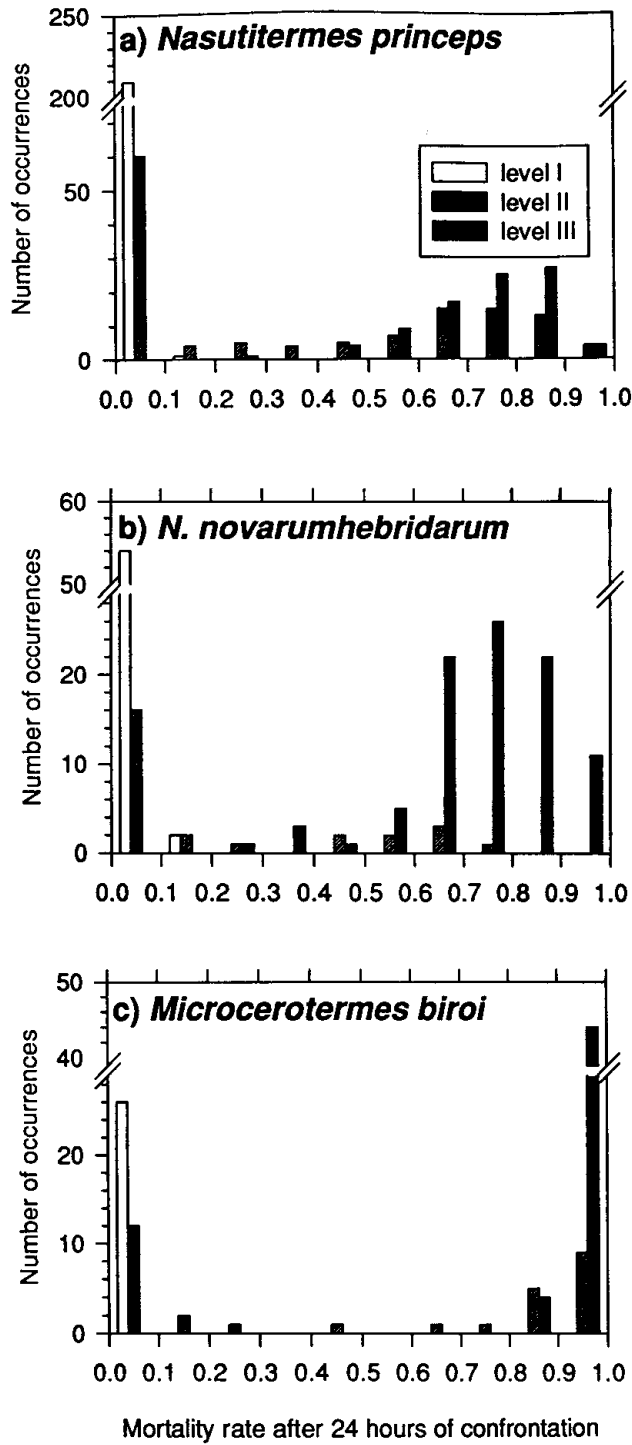
Fig. 2. Histogram of mortality rate due to anagonism (level I), moderate agonism (level II), and strong agonism (level III) after 24-h confrontation in laboratory bioassay for (a) *N. princeps*, (b) *N. novarumhebridarum*, and (c) *M. biroi* colonies.
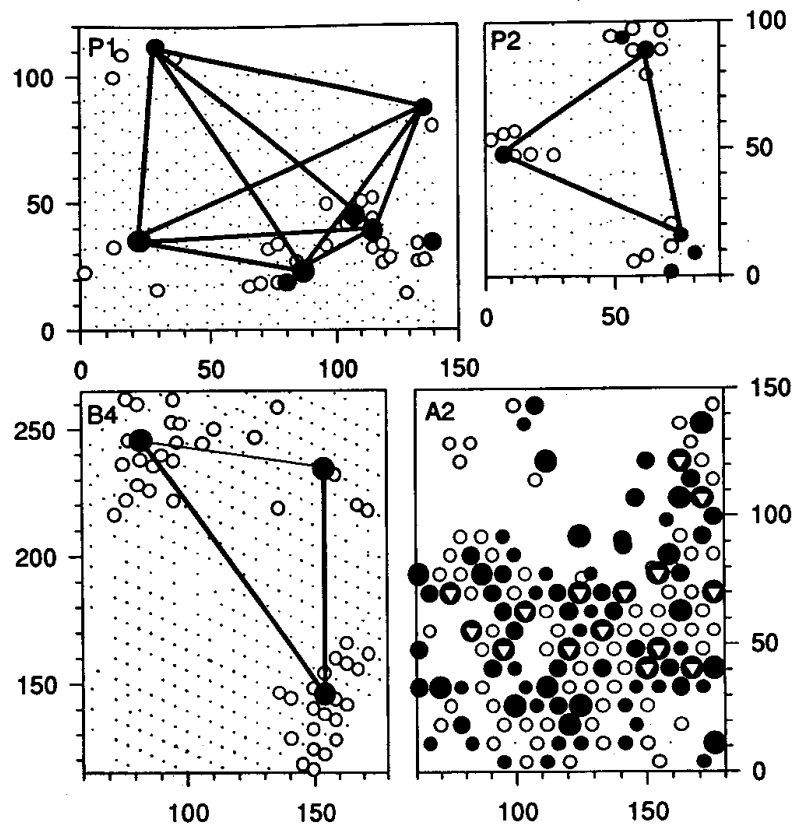
Fig. 3. Agonism between neighbor *N. princeps* colonies at four sites: P1, P2, B4, and A2. Filled circles, trees supporting a *N. princeps* nest; open circles, trees supporting *N. princeps* galleries; dots, trees not occupied by *N. princeps*. A thin line between two nests indicates absence of agonism (level I), and a thick line indicates agonism (level II or III). At site A2, 40 combinations between nests marked with a triangle yielded no agonism; for clarity corresponding thin lines were not drawn on the map.

containing large numbers of adultoid reproductives. At the three other sites, agonism (level II or III) was observed for 41 of 52 (79%) combinations tested. Moderate agonism occurred in 17 combinations, especially at site P1, where 9 of 10 confrontations were moderately agonistic. Lack of agonism was observed in 1 of 16 combinations between neighboring colonies (Fig. 3) and in 10 of 36 combinations (not represented in Fig. 3 for clarity) between geographically distant colonies. These proportions are not significantly different (Fisher's exact test, $P = 0.140$).

Agonistic reactions were consistent during the two consecutive seasons: 48 of 50 combinations tested in July–August 1991 yielded the same results in February–March 1992. In the two remaining combinations, between distant colonies coming from sites A2 and B4, agonism decreased (level III in 1991 to level II in 1992) or vanished (level II in 1991 to level I in 1992).

Agonistic Reactions Between Entire Nest Populations

Exploratory trails from *N. princeps* nests that were anagonistic in laboratory bioassays (I versus II and III versus IV, Table I) immediately huddled without aggressiveness when they encountered on the 9-m^2 experimental area. Foragers included workers, soldiers, nymphs, and, in the assay involving nests I and II, even alates. During the 9 days that these two confrontations lasted, exchanges of marked individuals between the nests were frequent, although this was sometimes interrupted by sunlight on termite foraging trails (which were not covered).

The outcome of encounters between two pairs of nests that were moderately agonistic in laboratory bioassays differed in the field (V versus VI and VII versus VIII, Table I). The first encounters between foragers coming from both paired nests resulted in many fights. However, in the confrontation involving nests V and VI, the allocolonial termites mixed 3 h later, whereas in the confrontation involving nests VII and VIII, allocolonial trails met again on several occasions but termites always fought and trails diverged afterward. Colonies V and VI remained in contact during the 13-day duration of the experiment, apparently because the number of aggressive individuals gradually decreased (presumably because they calmed down or were eliminated).

Individuals from two nests that were strongly agonistic in laboratory tests (IX versus X, Table I) also fought in seminatural conditions: battlefields up to 35 cm in radius, covered with corpses, were observed on several occasions and trails always diverged afterward.

All confronted nests were originally headed by reproductives; however, they died during the course of the experiment in three nests (Table I), either because the royal cell was damaged during the collection of the nest or because nests finally desiccated.

Agonism Between *N. novarumhebridarum* Colonies

Aggressive Behaviors

Individual aggressive behaviors in *N. novarumhebridarum* were similar to those observed in *N. princeps*. Death rates for anagonistic encounters (level I) were 0.03 ± 0.04 ($n = 56$) (Fig. 2b), which were not significantly different from those of controls 0.04 ± 0.04 ($n = 54$; $t = 0.86$, df $= 108$, $P = 0.390$). Death rates were variable in moderately agonistic (level II) encounters (0.22 ± 0.27; $n = 27$) and high (0.76 ± 0.14; $n = 91$) in strongly agonistic ones (level III) (Fig. 2b).

Frequency of Agonism in Laboratory Bioassays

Forty-one pairings between *N. novarumhebridarum* nests were performed in 1991, 25 of which were repeated the next season. Lack of agonism was

Table I. Comparison of Tests with Groups of Individuals in the Laboratory Versus Entire Nest Populations in a 9-m² Experimental Area

Nests, A vs. B	Laboratory agonism	First encounters	9-m² experimental area Outcome after 24 h	Reproductive status[a]	
				Nest A	Nest B
N. princeps					
I vs. II	Absent	Huddling	Exchange of neuters, nymphs, and alates	Polygynous	Polygynous
III vs. IV	Absent	Huddling	Exchange of neuters and nymphs	Polygynous	Polygynous ?[b]
V vs. VI	Moderate	Fighting	Exchange of neuters and nymphs	Polygynous ?[c]	?[c]
VII vs. VIII	Moderate	Fighting	Exclusion: trail divergence	Polygynous	Polygynous
IX vs. X	Strong	Fighting	Exclusion: trail divergence		
N. novarumhebridarum					
XI vs. XII	Absent	Huddling	Exchange of neuters and nymphs	Monogynous	Monogynous
M. biroi					
XIII vs. XIV	Not tested	Fighting	Nest attack	Queen(s) killed?	Polygynous
XV vs. XVI	Strong	Fighting	Nest attack	Monogynous	Queen(s) killed?
XVII vs. XVIII	Strong	Fighting	Exclusion: trail divergence	?	?

[a] Nests dissected at the end of the experimental period (4 days–3 weeks).
[b] Royal cell damaged during collection.
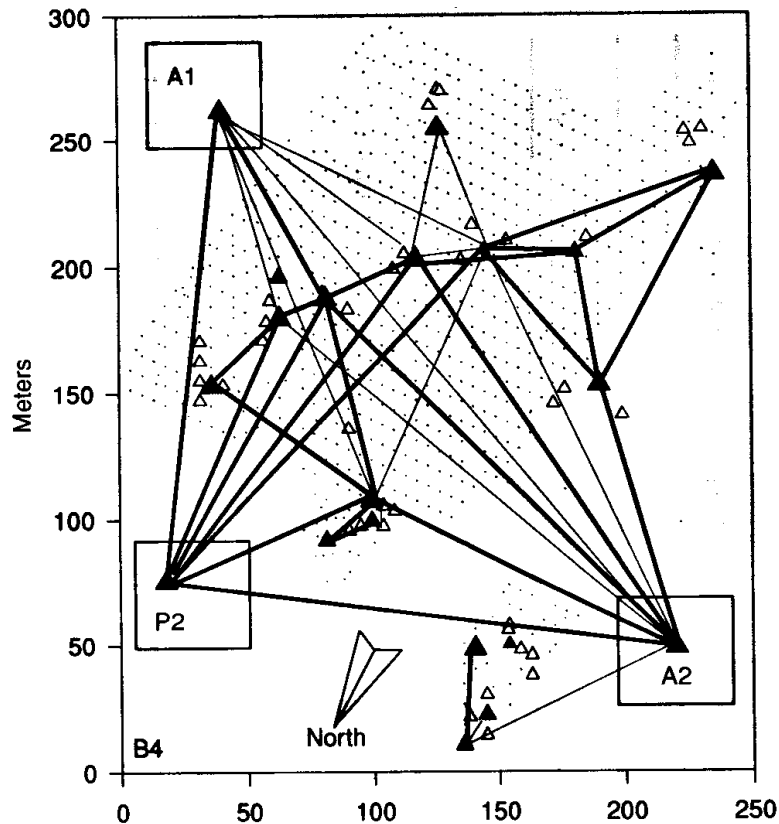[c] Nests died of desiccation.

Fig. 4. Agonism between neighbor *N. novarumhebridarum* colonies at site B4 and between these colonies and stranger colonies from sites A1, A2, and P2. Filled triangles, trees supporting a *N. novarumhebridarum* nest; open triangles, trees supporting *N. novarumhebridarum* galleries; dots, trees not occupied by *N. novarumhebridarum*. A thin line between two nests indicates absence of agonism (level I), and a thick line indicates agonism (level II or III).

observed in 6 of 21 combinations between strangers and in 8 of 20 combinations between neighbors (Fig. 4). These proportions are not significantly different (Pearson's χ^2 = 0.595, P = 0.440). Overall, agonism occurred in 27 of 41 (66%) combinations tested, comprising 4 cases of moderate agonism and 23 cases of strong agonism. Agonistic reactions were consistent in time: 24 of 25 combinations tested in June–July 1991 yielded the same results in March–April 1992. In one case, moderate instead of strong agonism was observed. Furthermore, nests XI and XII, which were anagonists in 1991, were confronted 3 years later and were still mutually tolerant.

Agonistic Reactions Between Entire Nest Populations

Foragers from both nest XI and nest XII (Table I), anagonists in laboratory, met without any manifestation of aggressiveness in the 9-m^2 experimental area.

The two nests remained connected during the 4-day duration of the experiment. The foraging trails were found partly covered 12 h after the first encounters and building activity continued afterward, although it sometimes was interrupted during the day because of direct sunlight exposure and predation by lizards.

Agonism Between *M. biroi* Colonies

Aggressive Behaviors

In contrast with the two *Nasutitermes* species, *M. biroi* soldiers are proportionally less numerous and use their large mandibles as mechanical weapons rather than squirting a defensive secretion. In anagonistic encounters (level I), termites behaved as controls: they were apparently mutually tolerant and showed some excitement (forward and backward body oscillation) when initially meeting the other group; this excitement disappeared as the two groups huddled. Allocolonial grooming (e.g., licking) was sometimes noticed during these anagonistic encounters. Death rates in anagonistic encounters were 0.01 ± 0.02 ($n = 26$) (Fig. 2c), which were not significantly different from those of controls (0.02 ± 0.02; $n = 32$; $t = 1.11$, df $= 56$, $P = 0.272$). In moderately agonistic encounters (level II), the death rates were strongly bimodal (0.50 ± 0.43; $n = 32$) (Fig. 2c). In some tests, only a few pairs fought among the mixed group. Because bites from workers or soldiers were often fatal, the few aggressive individuals usually died, leaving only tolerant individuals behind, which resulted in a low mortality. In other tests, aggressiveness appeared very gradually: individuals were apparently tolerant during the first encounters but started to nip or even to bite severely after 10 to 60 min of contact, resulting in a generalized battle with a high mortality. As in the two *Nasutitermes* species, replicates between moderately agonistic *M. biroi* colonies sometimes yielded very variable, apparently contradictory, results. In strongly agonistic encounters, general aggressiveness rose rapidly, resulting in a high death rate (0.96 ± 0.03; $n = 48$) (Fig. 2c). In two very agonistic encounters, 1 or 2 of the 12 soldiers present were observed banging their head on the substratum.

Frequency of Agonism in Laboratory Bioassays

Lack of agonism was observed in 1 of 14 combinations between nonneighbors (from sites N1 and P3) and in 8 of 21 combinations between neighbors at site N2 (Fisher's exact test, $P = 0.056$) (Fig. 5). Altogether, 26 of 35 (74%) combinations were agonistic. Moderate agonism was observed in nine of these agonistic combinations.

Agonistic Reactions Between Entire Nest Populations

Three pairs of *M. biroi* nests were confronted in seminatural conditions: two pairs exhibited strong agonism in laboratory bioassays (nests XV versus
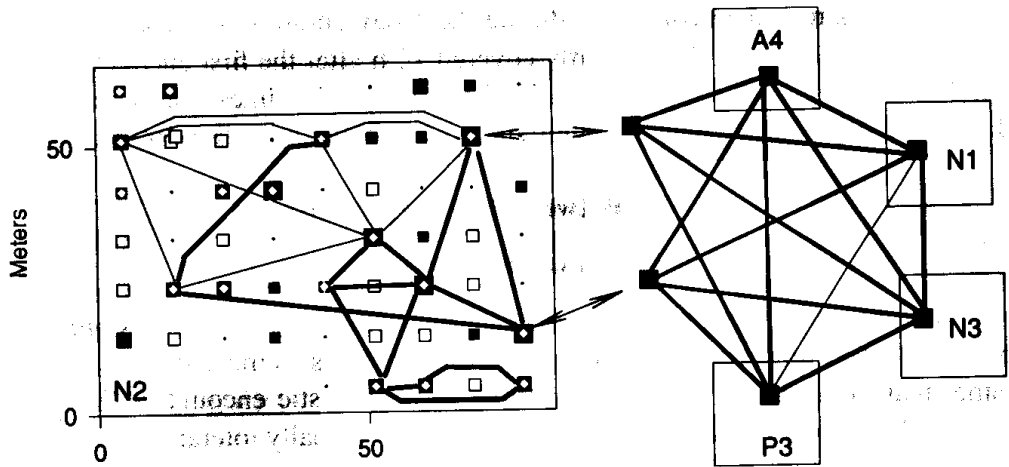
Fig. 5. Agonism between neighbor *M. biroi* colonies in site N2 and between two of these colonies and stranger colonies from sites A4, N1, N3, and P3. Filled squares, trees supporting a *M. biroi* nest; diamonds, nests with reproductives; open squares, trees covered with *M. biroi* galleries; dots, trees not occupied by *M. biroi*. A thin line between two nests indicates absence of agonism (level I), and a thick line indicates agonism (level II or III).

XVI and XVII versus XVIII, Table I); the other pair (nests XIII versus XIV, Table I), which was not tested in the laboratory, displayed aggressiveness in seminatural conditions.

When sticks departing from each nest were separated by only 15 cm at the ground level, confronted colonies (XIII versus XIV and XV versus XVI) tried to destroy each other. In both confrontations, a few hours after the first encounters, members from one nest built covered galleries in the direction of the stick leading to the other nest, which then was attacked. Fierce battles proceeded during the remainder of the experimental period. Thirteen days after the beginning of the confrontation, all four nests were dissected and found to contain live termites and egg masses. Both nest XIII and nest XIV contained corpses of fighters. Individuals from these two nests fought when combined in a petri dish arena. Only nest XIV was still headed by a queen. In contrast, individuals from nests XV and XVI no longer fought in laboratory bioassays. Nest XV still contained a queen and was devoid of corpses, but nest XVI lost its queen and contained many dead bodies.

When sticks departing from each nest were separated by 50 cm at the ground level (nest XVII versus XVIII, Table I), no nest attack was observed. At the beginning of the confrontations, trails from the two nests met at several points, resulting in fighting and leading to a rearrangement of each colony gallery network, which finally stabilized and diverged. During intense fights between allocolonial termites in the three pairings, the clicking sound of soldiers head-banging was heard in the nests.

DISCUSSION

Aggressive Behavior

Results of laboratory bioassays were consistent with the outcome of allo-colonial encounters in seminatural conditions: anagonistic *N. princeps* or *N. novarumhebridarum* groups joined, whereas strongly agonistic *N. princeps* or *M. biroi* groups avoided or tended to destroy each other. Moderately agonistic *N. princeps* colonies either joined after fighting or avoided each other.

Agonistic reactions between conspecific colonies of three arboreal-nesting termitids were variable, ranging from anagonism to strong agonism. Such variability has also been reported in other Termitidae (Andrews, 1911; Nel, 1968; Thorne, 1982a), in Rhinotermitidae (Su and Scheffrahn, 1988; Su and Haverty, 1991), in Termopsidae (Haverty and Thorne, 1989), and in Hodotermitidae (Nel, 1968). Whereas it was easy to define the lowest and highest grades of agonism (respectively, level I and level III), pairwise encounters also yielded a wide range of intermediate responses, which we called moderate agonism (level II). Su and Haverty (1991) also observed that in encounters between allocolonial *Coptotermes formosanus*, initially aggressive pairings could result in a low mortality, or conversely, some initially passive encounters could result in mortality due to fighting. These authors proposed that a stimulus eliciting initial aggression, received upon contact with an alien, must be reinforced by another stimulus for aggression to continue. The fact that the distribution of mortality rates was clearly bimodal, at least in *N. princeps* and *M. biroi*, pinpoints the existence of collective mechanisms leading either to the extinction of aggressive behaviors (as the most aggressive individuals calm down or are killed) or to their amplification until generalized fighting erupts. Such mechanisms of collective decisions are widespread in social insects, where their importance is best known in foraging and construction behavior; one of their general properties is a high sensitivity to past events (often random ones) and environmental conditions (Deneubourg and Goss, 1989). In the present case, the collective decision (i.e., whether alarm and aggressiveness will rise to generalized fighting or not) may depend on a large number of factors. Average aggressiveness or discriminatory ability may vary among colonies due to differences in genetic composition, age, health, nutrition, reproductive status, or environmental influences (Thorne, 1982a; Thorne and Haverty, 1991); individuals may vary within a colony for the same reasons; and even if it were possible to trigger confrontations repeatedly under similar conditions between the same groups of individuals, their outcome could vary by chance, depending on which individuals encountered each other and when. The fact that each colony is somehow heterogeneous itself (especially in polygynous and polydomous species, such as *N. princeps*) might explain why tolerance or rejection of members of another group is a matter of collective decision.

The participation of both soldiers and workers in colony defense is a common feature of termites (Andrews, 1911; Eisner *et al.*, 1976; Thorne, 1982a; Traniello and Beshers, 1985). *Nasutitermes* soldiers squirt a sticky defensive secretion on their enemies. The chemical composition of this secretion is colony specific (Pasteels *et al.*, 1988; Everaerts *et al.*, 1988; Roisin *et al.*, 1990), but it is not known if termites use it as a complementary cue to detect the presence of aliens. It has previously been shown that the frontal gland secretion acts as a pheromone in *N. princeps*, alarming and recruiting workers (Roisin *et al.*, 1990), but this secretion has no such pheromonal action in *N. novarumhebridarum* (unpublished results). *M. biroi* soldiers were observed banging their head against the substrate. This behavior was also noticed during interspecific encounters with *N. princeps* (Leponce *et al.*, 1996b). Although exceptional in laboratory bioassays, head-banging was observed during all three confrontations between entire nests of *M. biroi* when one of the nests was under attack. However, in these circumstances, it could have been triggered either by encounters with conspecifics, by encounters with predatory ants, or by mechanical disturbance caused by nest transportation.

Influence of Intraspecific Agonism on Community Structure

All three species showed comparable levels of intraspecific agonism: 79% of the combinations tested in *N. princeps*, 66% in *N. novarumhebridarum*, and 74% in *M. biroi* were agonistic. Agonism in *N. princeps* and *N. novarumhebridarum* did not vary seasonally, and in all three species, distant nests, unlikely to be genetically closely related, were not more often agonistic than nests from the same site. Intraspecific agonism should complement interspecific exclusion in shaping colony distribution in this community of arboreal termites.

Because of the high density of *M. biroi* colonies in plantations, encounters between foraging parties are very likely. For encounters between agonistic colonies, one of our experiments in seminatural conditions indicates that trails will probably diverge after fights. Nevertheless, when nests are too close, they apparently tend to eliminate each other: the colony from nest XIII attempted to invade nest XIV, whereas individuals from nest XV were apparently able to take over nest XVI (Table I). In the field, the fact that any single tree never supports more than one *M. biroi* colony (Leponce *et al.*, 1996a) constitutes evidence for competitive exclusion. However, the frequency of nest invasion remains uncertain. Neither actual fights between colonies of *M. biroi* nor signs of recent battles were ever witnessed in the field, in spite of the careful inspection of more than 2000 nests of this species. Some trees were found supporting two nests, one of which was headed by a royal pair, while the other contained an empty royal cell (Leponce *et al.*, 1996a): such findings may indicate that one colony killed the other, but it also may indicate colonization of a previously abandoned nest.

A likely hypothesis is that competitive exclusion most frequently eliminates young colonies before they have built an apparent nest but seldom leads to the death of a mature colony.

No naturally occurring fights were observed between mature colonies of *Nasutitermes* either. The scarcity of intercolonial fighting in *N. novarumhebridarum* can be explained by the relative sparseness of this species, which preferentially colonizes dead trees (Leponce *et al.*, 1995). Fights are probably more likely to occur between neighboring colonies of *N. princeps*, especially as those colonies attempt to expand their territory by constructing additional nests leading to polydomous colonies. However, such fights may be limited mostly to foraging trails and thus have little chance to proceed to nest elimination, except for the weakest (youngest, smallest) colonies. High densities of *N. princeps* nests such as in site A2 are probably possible only if nests are mutually anagonists, forming a supercolony. Supercolonies might also exist in other highly polygynous termite species such as *N. corniger*, *N. costalis*, and *N. polygynus*, where high nest concentrations have also been observed (Thorne, 1982b; Roisin and Pasteels, 1986b).

Trail divergence, consistent with other authors' data on neotropical species (Thorne, 1982a; Levings and Adams, 1984), is probably a mechanism to minimize warfare and allow each colony to maintain its own definite territory. The resulting pattern of territories observed in Neo-Guinean arboreal nesting termites (Leponce *et al.*, 1996b) recalls mosaics described in other termite communities (Levings and Adams, 1984; Jones, 1990, 1993; Jones and Trosset, 1991) and tropical ants (Majer, 1993; Adams, 1994).

Besides nest elimination or trail divergence, our experiments suggested that intercolonial encounters may have the outcome of colony fusion. This possibility was pinpointed by our experiments with *N. princeps* and *N. novarumhebridarum*. This phenomenon was actually observed by Su and Scheffrahn (1988) in *Coptotermes formosanus* in Florida. However, in that case, the involved colonies were part of a population most likely derived from a single recent introduction and, thus, highly related. Our experiments suggest that distant colonies of *N. princeps*, unlikely to be related, are sometimes anagonistic and are able to merge and to exchange alates. Considering the ability of *N. princeps* to produce two alate morphs (short- and long-winged) which readily assume reproduction in queenless nests (Roisin and Pasteels, 1985, 1986a), the possibility exists that transfer of alates may occur between neighboring colonies, leading to outbreeding without nuptial flights when alates become secondary reproductives during budding or replacement of reproductives. Genetic studies would be best suited to investigate this hypothesis, which casts doubt on the generally accepted rule that termite colonies are tightly closed to foreign genes (Roisin, 1993).

ACKNOWLEDGMENTS

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