Ins. Soc. 42: 129–136 (1995) 1015-1621/95/020129-08 $ 1.50 + 0.20/0

Importance of *Cubitermes* termitaries as shelter for alien incipient termite societies

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Key words: Foundation of societies, termites, biodiversity, soil fauna, rainforest.

Summary

We hypothetized that in the African rainforest (Cameroon), one of the principal limiting factors for termite multiplication is the relative scarcity of nesting sites. As a consequence, termitaries of *Cubitermes fungifaber*, *C. banksi* and *C. subarquatus* with their alveolate structure might constitute good shelters for incipient societies. In the cavities of these termitaries we recorded 29 termite species (including conspecifics) belonging to 23 genera and 5 subfamilies.

Active *Cubitermes fungifaber* and *C. banksi* termitaries shelter fewer incipient and adult societies than abandoned ones. Active *C. subarquatus* termitaries shelter more incipient societies than abandoned ones, while the difference is not significant with regards to termite societies at other stages of development.

The frequency of sheltered *Cubitermes* spp. incipient societies was so large (72.3%) that we suggest that abandoned termitaries and unoccupied zones of active ones had an adaptative value at the generic level as they constitute good shelters (probably the best) for incipient societies and favour reproduction in *Cubitermes* spp. societies.

Introduction

Measurements made in the Amazonian rainforest established that about one-third of the entire animal biomass is composed of ants and termites (Beck, 1971; Fittkau and Klinge, 1973). In African rainforests, termites and ants also represent the most important taxa in biomass. *Cubitermes* nests are very frequent and of great ecological importance (Baroni-Urbani et al., 1978; Dejean et al., 1986). Termites have a tendency to concentrate interspecifically in certain areas or to have mixed nests and as such have a patchy distribution. Also, some termite species are able to nest in alien termitaries where they benefit from a structure which permits them to build their own nest or squat in cavities of the host nest.

During ecological studies on the distribution of ground nesting ants conducted in 8 forests of southern Cameroon, the senior author noted that *Cubitermes* termitaries often sheltered alien termites, particularly incipient societies, whether they were inhabited by their termites or not. The frequency seemed so great that we hypothesized that the alveolate structure of these termitaries constituted good nesting sites for termites in the African rainforest, particularly for founding pairs.

C. fungifaber (Sjöstedt) and *C. banksi* (Emerson) are very common humivorous termites that build termitaries of 20 to 60 cm high that have a mushroom-like shape. *C. Fungifaber* is known to migrate in order to build a larger nest. So, abandoned termitaries are relatively frequent (Noirot et al., 1986). *Cubitermes subarquatus* Sjöstedt builds large termitaries covered by multiple caps reaching 160 cm high, generally inclined against large tree trunks (Grassé, 1984).

Material and methods

This study was conducted in Cameroon between 1987 and 1993 in the forest reserves of Campo (Mvini and Akok), Ottotomo and South Bakundu; the old secondary forests of Abong Mbang, Kala, Matomb, Ndupé und Zamakoé; and the gallery forest of Batchenga at Nzi.

To the evaluate of the density of *C. banksi* and *C. fungifaber* termitaries, we counted the number of termitaries on 42 plots of land 625 m^2 (25 × 25 m) randomly selected in the forests of Ottotomo (8 plots), Nzi (4 plots), Akok (16 plots), Mvini (4 plots) and Ndupe (10 plots). In order to evaluate the density of *C. subarquatus* termitaries, we proceeded in the same way on 35 parcels in Ottotomo (8 plots), Kala (10 plots), Matomb (7 plots) and Ndupe (10 plots).

For the research on alien societies, 725 termitaries of *C. banksi* and *C. fungifaber* were randomly selected in different zones of the forests. We distinguished active termitaries (358) from abandoned ones (367). Each mound was subjected to a complete and thorough dissection in order to discover small pockets of secondary inhabitants. For *C. subarquatus,* we broke open 65 active termitaries (between 70 and 120 cm high) randomly selected in different zones of the forests. Abandoned termitaries of this species being rare, we were obliged to extend our study area to include the entire forest.

Among societies sheltered in the *Cubitermes* nests, we distinguished "incipient societies" composed of the founding pair which can be surrounded by eggs, larvae and, eventually, no more than 20 workers; "young societies" with the founding pair, eggs, larvae, sometimes the first soldiers and between 20 and 100 workers; "large societies" as in the preceding case but with a physogastric queen, some soldiers and more than 100 workers; "adult societies" similar to large societies but with the presence of winged sexuals; and "parts of societies" composed of numerous workers and some soldiers.

When alien termites were present, samples were captured with an aspirator and preserved in small glass tubes filled with alcohol (60 percent). Voucher specimens of termite species mentioned in this survey were sent to the Musée royal de l'Afrique centrale, Tervuren.

Statistics. For comparisons of the frequency of alien societies sheltered in the different termitaries, we used the Student t-test. For comparisons of percentages, we used contingency tables and the Fisher exact test or the Chi square test.

Results and discussion

Evaluation of the density of the Cubitermes termitaries

On the 42 plots studied, we found a total of 327 termitaries of *C. banksi* and *C. fungifaber*; 48.6% were active and 51.4% were abandoned. The number of termitaries per plot varied from 2 to 14, the mean being 7.78±0.85 termitaries, corresponding to 124.48±13.6 termitaries per hectare (60.6±8 active ones per hectare). For *C. subarquatus* termitaries, we found 73 active termitaries on the 35 plots studied. The number of termitaries per plot varied from 0 to 4, the mean being 2.08±0.49 termitaries, corresponding to 33.4±7.8 active termitaries per hectare. In total, we found 94.2±8.4 active *Cubitermes* spp. termitaries per hectare from parcels where both kinds of termitaries were recorded.

These values are lower than estimates by Hebrant (1970 in Baroni-Urbani et al., 1978) on *C. exiguus*, a savanna species and Dejean et al. (1986) on *Cubitermes* spp. in a secondary forest, who found 510 and 650 termitaries per hectare respectively. It appears therefore, that the density of *Cubitermes* nests varies greatly from one place to another.

We broke open 725 *C. banksi* and *C. fungifaber* and 100 *C. subarquatus* termitaries (corresponds to areas of approximately 5.8 and 3 hectares, respectively).

Alien termite species squatting C. suarquatus termitaries

Diversity of species. *Cubitermes* spp. nests shelter 29 alien species (including conspecifics; Table 1) belonging to 23 genera and 5 subfamilies. Ernst (1960) also noted that alien termite species sheltered in both abandoned and active *Cubitermes* termitaries of East Africa. He found, in order of frequency: *Microcerotermes,* several *Cubitermes, Microtermes, Ancistrotermes, Amitermes, Noditermes, Crenetermes, Euchilotermes, Trinervitermes, Procubitermes, Termes* and *Promitrotermes*. In Kinshasa, Zaïre, Bouillon (1964) systematically found *Microcerotermes* spp. under *C. exiguus* nests and Bodot (1966, in Grassé, 1984) observed the invasion of *C. severus* nests by *Amitermes evuncifer*. Among the most frequent termite squatters indexed here, *Cubitermes* spp. were known to shelter in alien congeneric nests (Ernst, 1960) and *Microtermes* spp. frequently squat in termitaries of *Cubitermes*, Macrotermitinae and Nasutitermitinae (Grassé, 1984). Present results give a wider range of possibilities with *Protermes prorepens* being the most frequently observed. This is the first time that this genus is reportred as a squatter of other termites.

Incipient societies and the majority of societies at other stages of development sheltered directly in the cavities of the host termitaries, but *Microtermes* spp. and *Protermes prorepens* build their own structure, as has been previously noted for *Noditermes* and *Crenetermes* (Ernst, 1969).

Table 1. Stage of development of the alien societies sheltered in the *Cubitermes* nests (I; Y; L; A Part.: incipient, young, large, adult and part of societies) and comparison of the rate alien societies, at other stage than incipient, sheltered in the *Cubitermes* termitaries (Act.; Ab.: active and abandoned nests).
Statistical comparisons. Alien societies sheltered in active versus abandoned termitaries: *C. banksi/C. fungifaber*: $t = 6.9 > 3.3$; $P < 0.001$; *C. subarquatus*: $t = 0.5 < 1.9$; N.S. Termitaries of *C. banksi/C. fungifaber* versus *C. subarquatus*: active: $t = 12.8 > 3.3$; $P < 0.001$; abandoned: $t = 5.4 > 3.3$; $P < 0.001$

	Stages of the societies sheltered					***C. banksi/ C. fungifa.***		***C. subarquat.***	
Alien species recorded	I	Y	L	Ad.	Part	Act.	Ab.	Act.	Ab.
Rhinotermitidae; Coptotermitinae									
Coptotermes cf. *sjoestedti* Holmgren			3			2			1
Termitidae; Apicotermitinae									
Apagotermes stolidus Sands			2		2			3	1
Termitidae; Termitinae									
Crenetermes albotarsalis (Sjöstedt)			1				1		
Cubitermes spp.	353	7	7	1		4	4	7	
Cubitermes subcrenulatus Silvestri			1					1	
Fastigitermes jucundus (Sjöstedt)					1			1	
Furculitermes parviceps Emerson					4		2		2
Furculitermes winifredae Emerson		1	3		6		4	6	
Microcerotermes sp.			1				1		
Nitiditermes sp.			1				1		
Noditermes sp.			1				1		
Ophiotermes mandibularis (Sjöstedt)		2	15	3		1	6	10	3
Orthotermes mansuetus (Sjöstedt)					1			1	
Pericapritermes sp.					3		3		
Pericapritermes urgens Silvestri					6			3	3
Procubitermes sp.		1							1
Thoracotermes thoracothorax		1					1		
Termitidae; Macrotermitinae									
Acanthotermes acanthothorax (Sjöstedt)					11		7		4
Macrotermes subhyalinus (Rambur)					1		1		
Macrotermes muelleri (Sjöstedt)	1						1		
Microtermes spp.					1	12	36	8	4
Odontotermes cf. *patruus* (Sjöstedt)	30	7	41	12			4		3
Protermes prorepens (Sjöstedt)					7	18	41	8	6
Pseudacanthotermes militaris (Hagen)		11	54	8			1		
Termitidae; Nasutitermitinae					1	2	3		
Nasutitermes latifrons Sjöstedt		5					2		
Fulleritermes sp.					2		2		2
Leptomyxotermes doriae (Silvestri)					4		1		
Undetermined	104	21			1	7	12		2
N⁰ of alien societies sheltered	488	56	130	24	51	44	137	49	31
Total	488 incipient + 261 = 749					261			
N⁰ of termitaries sheltering alien soc.			331			44	126	47	27
N⁰ of termitaries opened			825			358	367	65	35

Table 2. Comparison of the frequencies of incipient termite societies sheltered in the *Cubitermes* termitaries. Statistical comparisons.

1) Comparisons of frequencies of termitaries sheltering incipient societies. Active versus abandoned mounds; for *C. banksi/C. fungifaber*: $X^2 = 19.6 > 19.5$; $P < 10^{-5}$; for *C. subarquatus* 100% in both cases; between active termitaries of *C. banksi/C. fungifaber* and *C. subarquatus*: $X^2 = 242.7 > 37.3$; $P < 10^{-9}$; for abandoned termitaries: $X^2 = 91.9$; $P < 10^{-9}$.
2) Incipient societies distribution. Active versus abandoned termitaries: *C. banksi/C. fungifaber*: $t = 4.4 > 3.3$; $P < 0.001$; *C. subarquatus*: $t = 4.1 > 3.3$; $P < 0.001$.
   Termitaries of *C. banksi/C.fungifaber* versus *C. subarquatus*. Active mounds: $t = 26.2 > 3.3$; $P < 0.001$; abandoned mounds: $t = 26.2 > 3.3$; $P < 0.001$

Incipient societies	*C. banksi/C. fungifaber*		*C. subarquatus*	
Alien species recorded	Active nest	Aband. nest	Active nest	Aband. nest
Cubitermes spp.	22 (6.1%)	54 (14.7%)	201 (304%)	76 (217%)
Microtermes spp.	5 (1.4%)	13 (3.5%)	8 (12.3%)	4 (11.4%)
Macrotermes spp.				1 (2.8%)
Indetermined	10 (2.8%)	21 (5.7%)	54 (83.1%)	19 (54.3%)
N⁰ of termitaries opened	358	367	65	35
N⁰/termit. shelter. incipient soc.	35 (9.8%)	80 (21.8%)	65 (100%)	35 (100%)
N⁰ of incipient societies sheltered	37	88	263	100

***Cubitermes* termitaries as shelter for incipient societies.** In total, 488 incipient societies were recorded, belonging principally (72.3%) to *C. banksi, C. fungifaber, C. subarquatus* and *C. subcrenulatus* species. Each of the 100 *C. subarquatus* termitaries sheltered incipient societies while for *C. banksi/C. fungifaber* the rate was 9.8% and 21.8% respectively for active and abandoned termitaries, the differences being significant (Table 1 and 2).

Active *C. banksi/C. fungifaber* termitaries sheltered fewer incipient societies than abandoned ones while we found the reverse was true for *C. subarquatus* ($P < 0.001$ in both cases). Active *C. subarquatus* nests sheltered more incipient societies than active or abandoned *C. banksi/C. fungifaber* termitaries (Table 2).

***Cubitermes* termitaries as shelter for alien societies at stages other than foundation.** Here also, active *C. banksi/C. fungifaber* termitaries sheltered fewer alien societies than abandoned ones, but for *C. subarquatus* the difference is not significant (Table 1). The large size of *C. subarquatus* termitaries with entire zones abandoned to erosion by their inhabitants allows numerous squatters to enter, while in *C. banksi/C. fungifaber* termitaries this phenomenon is rare and limited to the cap which shelters most of the incipient societies; alien societies at other stages of development shelter principally at the base of the nest.

Stages of alien societies squatting *Cubitermes* termitaries. Incipient societies are by far the most frequent (488 for a total of 749 incipient societies; 65.1%). Other stages of development of the societies are also presented (young, large and adult societies) so that we can argue that in certain cases the whole life cycle of a society can unroll as squatter. This seems true for *Cubitermes* spp., *Microtermes* spp., *Ophiotermes mandibularis* and *Protermes prorepens* (in both of the latter cases, incipient societies are indexed as "undetermined" in Table 1).

According to Grassé (1984), the concentration of termites in certain areas with mixed nests of several species belonging to different subfamilies is probably the consequence of founding pairs having been attracted by zones where other termites, regardless of the species, were nesting. Present results agree with this assertion, but the rate of *Cubitermes* spp. incipient societies recorded was too great to be due to chance, since the forest floor shelters numerous Macrotermitinae and Apicotermitinae in whom the production of winged sexuals during swarming is superior to *Cubitermes* spp. Also, Nasutitermitinae production is very important in rain forests. If incipient societies were randomly distributed, free cavities of *Cubitermes* nests would shelter a wider range of Macrotermitinae, Apicotermitinae and Nasutitermitinae. Another argument for founding pairs being attracted by congeneric nests is provided by samples taken by Bolton et al. (1992) who found 119 *Cubitermes* incipient societies in congeneric nests and none on the forest floor (43 m^2 sampled) or in fallen, rotten branches in the Campo forest reserve (Southern Cameroon).

After founding pairs shelter in congeneric termitaries, they begin their life cycle as squatters and two non-exclusive possibilities can occur.

1) When the society reaches a certain size, it migrates to build its own termitary. This scenario is true for *C. fungifaber* which migrates frequently to build new nests (Noirot et al., 1986) and probably for *C. banksi* (active nests frequently surrounded by abandoned ones in the present observations).

2) Newly-abandoned termitaries shelter incipient societies that then grow and occupy most of the cavities. In this situation the same termitary can be occupied successively by the true "owner" and by a squatter that appears to be an "owner", but which can belong to a different species. This was probably the case for the three *C. subarquatus* termitaries completely invaded by *Ophiotermes mandibularis* in the present results. This phenomenon probably occurs between homo- and heterospecific *Cubitermes*. For instance, we found "young societies" squatting in termitaries devoid of their "owners" and we indexed them as alien thanks to their small size. So, it is possible that certain "active termitaries" in the present results were actually inhabited by alien societies.

Parts of societies which live in active or abandoned termitaries concern 15 species. This previously described phenomenon (Grassé, 1984) can concern:

1) societies that first sheltered in the host nest and then spread out, or
2) societies that invaded the host termitary as in the case of *Amitermes evuncifer* occupying a *C. severus* nest (Bodot, 1966 in Grassé, 1984).

The role of doryline ants

We were present 7 times during an invasion by doryline ants (*Dorylus* spp.). In two cases, we saw the beginning of the attack. Little by little doryline workers invaded entire galleries and cavities of nests. In three another cases, the invasion was completed by the time we broke open a nest of *C. banksi* and we noted that two cavities sheltering *Camponotus* spp. incipient societies were spared. Two *C. subarqutus* nests containing only doryline ants were also observed, and in these cases, squatter ants such as *Platythyrea modesta* and *Camponotus* spp. migrated while the termites (and perhaps other ants) were completely destroyed.

It is known that in reaction attacks by doryline ants, *Cubitermes* spp. generally fight to the finish (Wood and Sands, 1978), but the ruptured bodies of *C. ugandensis* and *C. testaceus* workers are distasteful and impede attacks of *Anomma kohli* (Williams, 1959).

Conclusion

Our results show that founding pairs of *Cubitermes* spp. have a tendency to find shelter in abandoned or active congeneric nests which probably have an adaptative value in furnishing good shelter in habitat poor in other possibilities, even though founding pairs are able to dig their copularium directly in the soil. But they can be inundated or easily unearthed by predators such as ants (other than Dorylinae), while termitary cavities are rarely invaded by rain water and their partitions are too hard to be easily destroyed.

Selection pressure is often considered as a criterion permitting a correlation between the characteristics of habitats with those of the organisms living within them. In the present situation congeneric termitaries provide good shelters for their offspring and thus favour the multiplication of the societies. So, the founding pairs are not submitted to selective pressure due to the scarcity of nesting sites in the other places in the environment where other termites compete. The originality of this phenomenon consists of the fact that this benefit occurs at the generic level since one founding pair of *Cubitermes* can find shelter in termitaries of several congeneric species.

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Received 13 July 1994;
revised 5 November 1994;
accepted 14 November 1994.