

**FORAGING OF MACROTERMES SPP.
(ISOPTERA : MACROTERMITINAE) IN THE TROPICS**

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SUMMARY

The Macrotermitinae have a dominant position in most tropical savannas ecosystems.

Macrotermes species, thanks to their symbiosis with a fungus, are able to collect a wide range of plant materials. They have very large nest populations and their energy budget and castes ratios have probably an adaptative value.

On the large territory of each nest, the termite is able to realize both an energy maximization of the food collected (by switching the foraging area throughout the season) and a time minimization (forage being collected in two phases : firstly above ground and stored underground, and secondly conveyed to the nest centre). This foraging territory has a more or less permanent underground structure, leading certainly to a strong influence on the ecosystem : in soil processes and populations control.

The periodic variation of the foraging activity involves day-night cycles and seasonal periodicity. The main foraging takes place in the dry season, for the sexual brood to mature and be ready by the outset of the rainy season.

As far as their reproduction is concerned, *Macrotermes* spp. are «r» strategists. Furthermore, their symbiosis with *Termitomyces* allows them to behave as ultrageneralists : they are then perfectly adapted to fluctuating tropical ecosystems.

RÉSUMÉ

La récolte de nourriture de *Macrotermes* spp. sous les Tropiques

Grâce à la mise en place de stratégies de récolte particulières, les Macrotermitinae dominent les populations de termites dans la plupart des écosystèmes de savane des zones éthiopienne et indo-malaisienne.

La symbiose avec le champignon (*Termitomyces*) leur permet la récolte d'un large éventail végétal, la digestion de ce matériel et son enrichissement relatif en éléments nutritifs (azote). Leurs colonies très peuplées (10^6 à 3×10^6), où l'énergie est recyclée, peuvent faire face aux périodes rigoureuses en augmentant le nombre d'ouvriers en récolte. Les proportions des différentes castes ainsi que le budget de la récolte ont certainement une valeur adaptative, les différences entre castes de *Macrotermes* devenant plus tranchées lorsque le milieu devient plus fluctuant.

Chez certaines espèces de *Macrotermes*, la récolte s'effectue en deux temps : tout d'abord une collecte à la surface du sol et un stockage souterrain, puis un retour au nid. Ceci permet de minimiser le temps nécessaire pour récolter l'énergie utile (ainsi que l'exposition aux prédateurs). D'autre part, la dimension du territoire de récolte, qui semble plus ou moins constant chez les *Macrotermes* de savane (1100 - 3100 m²) et le déplacement journalier de la zone récoltée à l'intérieur de ce territoire, maximisent l'énergie recueillie par les termites.

Ce territoire de récolte possède une structure plus ou moins permanente, formée de galeries rayonnantes circulant à 10 - 15 cm sous la surface du sol et débouchant à l'extérieur par des trous de récolte, qui joue certainement un rôle dans la compétition intra- et inter- spécifique.

La comparaison entre les cycles saisonniers de récolte de 4 espèces de *Macrotermes* montre que dans tous les cas, l'activité de récolte maximale se place durant la saison sèche, afin d'assurer la maturation du couvain de sexués qui essaïmera durant les pluies.

Le mécanisme régulateur des réserves de meules à champignons est sans nul doute un point essentiel du succès des Macrotermitinae dans les écosystèmes fluctuants tropicaux. En ce qui concerne leur reproduction, cette sous-famille possède une stratégie «r», ce qui, en plus d'un régime ultragénéraliste, leur confère toutes les caractéristiques des espèces colonisatrices.

Recent works indicated the dominant position of the fungus-growing termites in tropical ecosystems, ranging from the Sahel savanna to the Malayan rain forest. The Macrotermitinae represent 37 to 75 % of the total termite live-weight biomass (Josens, 1972, 1974 ; Lepage, 1974a ; Wood & al., 1977 ; Abe, 1979).

The main features of the foraging activities of two *Macrotermes* species have been studied in two semi-arid ecosystems : *M. subhyalinus* Rambur in North Sénégal (Lepage, 1972, 1974a & b) and *M. michaelsoni* Sjöstedt in Kenya (Lepage, 1977, 1979, 1981a & b). From the results obtained, it is possible to make some general comments on foraging and feeding within the subfamily Macrotermitinae.

FORAGING STRATEGIES

The Macrotermitinae have evolved several strategies which probably explain their success as evidenced by their high populations and consumption.

Symbiosis with fungus

In all cases, the relative importance of the Macrotermitinae increases when their consumption is taken into account. This is because they have higher weight-specific consumption rates than other Termitidae, as a result of their symbiosis with fungi (Wood, 1978). All aspects of this association have been summarized by Sands (1969). The ecological advantages of growing fungus gardens have recently been pointed out by Cherrett (1980) for the Ants of the subfamily Attini. Broadly, the challenge for the insects is to produce protein-rich tissue from protein-poor food, a hard task for species feeding mainly on litter, like the Macrotermitinae. Table I, established from the data of Matsumoto (1976), shows how the symbiosis with the fungus increases step by step the amount of nitrogen available to the termite :

Table I – Nitrogen content (% of dry weight) and C/N ratio of the food cycling within the nest of *Macrotermes carbonarius* (from Matsumoto, 1976).

Tableau I – Contenu en azote (en % du poids sec) et rapport C/N de la nourriture recyclée à l'intérieur du nid de *Macrotermes carbonarius* (d'après Matsumoto, 1976).

| Source | Nitrogen % | C/N |
|--|------------|------|
| Fragments of leaves stored in the nest | 1.3 | 34.3 |
| Fungus comb | 1.7 | 25.5 |
| Conidiophores | 7.3 | 6.2 |
| Termite major worker | 10.0 | 4.6 |
| Termite major soldier | 11.1 | 4.1 |

Also, the termite can collect a wide range of plant material although the competitive advantage is not so obvious for termites as for ants, since the former feed mostly on plants at various stages of decomposition (La Fage & Nutting, 1978). Being ultra-generalists is a great advantage in changing tropical systems. Furthermore, the fungus garden acts as an energy pool and buffering mechanism (food supply, temperature, humidity) between the termite colony and its environment.

Nest populations

In savanna ecosystems, the *Macrotermes* mound builders have large populations : mature nests may contain between 10^6 and 3.10^6 individuals (up to 5 1/4 million for *M. michaelseni* in Kenya, Darlington, 1982a). Such high concentration of workers is able to achieve sophisticated homeostatic mechanisms to regulate the temperature and aeration of the nest. The pool of workers is the pathway of a constant recycling of energy. This population has probably evolved under the «principle of stringency», as outlined by Wilson (1975) : the energy budget of the colony is devised to face periods of greatest stringency, where higher numbers of workers are able to search for and to collect food.

Energy budget and castes proportions

As stressed by Wilson (1975), the population structure of social insects has an adaptative value. As far as foraging is concerned, there seem to be at least two main strategies among the species of Termitidae which forage above-ground. They can either forage in the open air, escorted by many soldiers with powerful chemical and/or mechanical weapons, or they can forage mostly under cover in tunnels or galleries or under soil sheeting. That is to say they must use either more anti-predation energy or more building energy. The first strategy is best illustrated by the *Trinervitermes* spp. and the second by most of the Macrotermitinae in arid environments. In the Malayan forest the species which forage under cover have a lower percentage of soldiers (1.2 - 2.8 %) than the ones foraging in the open (17.2 - 29.6 %) (from the data of Abe, 1979 and Abe & Matsumoto, 1979).

Considering the genus *Macrotermes* only, it seems that an decreasing proportion of the energy budget is devoted to soldiers as the environment becomes less humid. Soldiers represented 19.7 % by dry weight of total sterile adults for *M. carbonarius* in West-Malaysia (Matsumoto, 1976 ; 12.7 % for *M. michaelseni* in Kenya (Darlington, 1982a) and only 8.5 % for *M. subhyalinus* in the Sahel (Lepage, 1974a).

Most probably, a better efficiency of the *Macrotermes* colony is due to an optimization of castes rations : the diversification (in numbers and weights) of these castes is well achieved as compared with other Macrotermitinae (i.e. : *Microtermes*). We might expect that differences in sizes and roles between castes in *Macrotermes* species would be less obvious where the tropical environment is less variable (eg forest as compared with savanna). From the few examples available, the weight-ratio between extremes of castes (major soldier versus minor worker) is about 5.0 for *M. carbonarius* in a rain-forest (Matsumoto, 1976), 8.2 for *M. bellicosus* in a southern guinean savanna (Collins, 1977, 1981) and 16.2 for *M. subhyalinus* in a Sahel savanna (Lepage, 1974a). These data agree with Wilson's (1975) statements on ergonomics of castes in social insects.

Territory and foraging behaviour

The foraging behaviour is rather constant in the genus *Macrotermes* (at least in savanna ecosystems) : the foraging populations flow in a network of underground galleries, emerging on the ground surface through foraging holes to collect plant materials back to their nest. Soil shelters, tunnels or trails may be added outside the foraging holes.

The underground network is more or less permanent and defines the territory of the colony, the area where the foraging population collects the available food. Thanks to the possession of such a territory, the termite is able to realize two foraging strategies which are somewhat contradictory for most other insect species :

– Energy maximization (as exposed by Schoener, 1971), which becomes possible on the large territory of a single colony, covering a wide range of habitats, by switching the area foraged every few days and so collecting almost all the food available.

– Time minimization (Schoener, 1971), which consists of minimizing the amount of time required to harvest and secure the available energy. *Macrotermes* workers (especially the majors have large mandibles for carrying large pieces of plant back to the foraging holes and storing them underground. They also come out in great numbers at peaks of foraging activity (cf Nest populations). In that respect, many species of termites forage in two phases. In the first, forage is collected above ground and stored, in the second it is conveyed to the nest centre. An example of this strategy is *Hodotermes mossambicus* (Leuthold, 1973). The same appeared to be true for *Macrotermes michaelsoni* in Kenya (Lepage, 1981a, Darlington, 1982a & b). More data being needed to find out if this strategy is also followed in other species of *Macrotermes* where no macerated food materials have been found in nests.

The time minimization behaviour acts also as predation minimization : breaking down of forage into smaller pieces occurs below-ground, where the workers are protected from predators.

THE FORAGING TERRITORY

Structure of the territory

Many authors have noted the underground gallery systems of termite colonies (Fuller, 1915 ; Greaves, 1962 ; Ratcliffe & Greaves, 1940), but the detail and extent of the systems have rarely been measured.

A very interesting study by Darlington (1982b) has recently brought much new information about the underground foraging system of *Macrotermes michaelseni* nests in Kenya. A few large radial passages extend outwards at a depth of 50 - 80 cm for up to 10 m from the mound, then rise steeply and level off at 9 - 15 cm below soil level. Here they branch and interconnect to form a network of horizontal passages containing many storage pits. Steep branches lead up to soil surface where they end at foraging holes (which are sealed when not in use). Beyond 30 - 40 m from the mound, the network peters out into blind-ending peripheral passages. Altogether this structure may total about 6 000 m of passages per mound and 72 000 storage pits. Furthermore, Lepage (1977) recorded an average of 22 000 to 50 000 foraging holes per mound. This foraging system has certainly a strong influence in the ecosystem. In the area studied in Kenya, the mounds density reached 4 per ha, or a total of 17 km underground passages, 190 000 storages pits and more than 150 000 foraging holes (Darlington, 1982b and pers. comm. ; Lepage, 1977, 1981a).

Size of the territory

We would expect a positive relationship between the population of the colony and the size of its territory : Banerjee (1975) found a linear relationship between the mound height (proportional to the population) and the size of the colony territory, in *Odontotermes redemani*.

The territory of a mature colony of *Macrotermes* seems rather similar even in different ecosystems : 1 100 m² in Sénégal (Lepage, 1974) to 3 100 m² in Nigeria (Wood & Ohiagu, 1976). The number of foraging holes per nest is also similar : up to 50 000 in Kenya (Lepage, 1977), 30 to 40 000 in Sénégal (Lepage, 1974a). However, the intensity of foraging in a given area can vary, as is shown for example by the density of foraging holes, 10-15 /m² both in Kenya and Nigeria, but higher in the Sahel savanna : 20-60 /m².

Periodic variation of the foraging area

In one particular night, the workers forage only in a small part of the territory ; the total area foraged per month in Kenya, for *Macrotermes michaelseni*, was 133 m² in February and 600 m² in July (Lepage, 1977). This pattern, night after night, achieved a nearly full exploitation of the area.

Territory and competition

Such territories certainly play a key role in regulating the populations, as concluded by Kluijver & Tinbergen (1953) : with a density of 1.9 m of underground passage per m², some young nests are probably prevented from establishing themselves. Probably the food supply is the ultimate limiting factor, as stated by Wilson (1975) and argued also by Wynne-Edwards (1962). In this hypothesis, one of the function of territory in *Macrotermes* would be to limit the populations.

Darlington's observations (1982a & b) corroborate this hypothesis : she established that a territory is somewhat «alive» as the old passages of an old mound, 28 m from the nest studied, were incorporated into the passages of the living nest. In other cases, an old nest could be taken over and therefore used as subsidiary chambers for growing fungus-combs.

Lepage (unpublished observations) estimated an intra-specific predation of nearly 10 % on established young field colonies of *M. michaelseni*. Bouillon (1970) reported Mathot (unpublished observations) on a nest of *M. bellicosus* near Kinshasa which was not approached by nests of *Cubitermes sankuriensis* because of the territory of the *Macrotermes* mound. Lepage (unpublished observations) recorded real densities of mounds on 14 plots (1.5 to 3.9 mounds/ha), together with their nearest neighbouring distances and the number of trees (50 to 492/ha). Mounds were overdispersed at all site, probably because of their territoriality but a highly negative relationship was found between the mounds overdispersion (departure from a random distribution) and the number of trees per average nest (which could be a rough estimation of habitat diversity). In other words, in a diversified environment, the mounds tend to be randomly distributed.

PERIODIC VARIATION OF THE FORAGING ACTIVITY

Daily activity

Bouillon (1970) proposed the hypothesis that foraging tends to occur in termites when the outside temperature departs the least from the temperature

within the nest. Since the temperature within *Macrotermes* nests is around 28 - 30°C (Ruelle, 1964) this hypothesis is rarely realised, except maybe in Sahel, where *M. subhyalinus* started its activity in the evening at 25°C in January and 32°C in March (Lepage, 1974a), the peak of activity occurred between 22 h 30 and 0 h 45 (at 23 to 26°C). In Mokwa (Nigeria), *M. subhyalinus* never started foraging before 21 h (Wood, 1978). It appears that each species of termite reacted to the temperature cycle of its own distribution area : *M. michaelseni* foraged in colder conditions in Kenya than *M. subhyalinus* in Sénégal. Broadly, high temperatures prevent foraging in the evening and low temperatures stop foraging in the early morning.

In the case of *Macrotermes michaelseni*, as stated above, the foraging activity was split into two phases : one above the ground, the more obvious, strongly affected by temperature and evaporation and probably by predation, and the other under the ground, much more inconspicuous. A special device was used in Kenya to study this underground activity (Lepage, 1977, 1981a) : a single nest was surrounded by a trench and the broken underground galleries were reconnected by clear plastic tubes in which the in- and out-going foraging populations were counted at intervals. The total population outside the nest was determined from the balance between the in- and out-going populations. From the comparison between the populations, above and below the ground, two conclusions can be drawn : first, there is a good relationship between the two foraging populations. At the night peak of foraging, about half of the population never appeared above the ground. But secondly, the underground activity continued before and after, when the above-ground activity had ceased and when the foraging holes were closed. From these comparisons, foraging in two phases has been postulated, as quoted above (Lepage, 1981a), corroborated by the fact that the in-going workers were never seen carrying large pieces of food in their jaws but most smaller fragments. The later discovery of storage pits by Darlington (1982b) supported the hypothesis.

Seasonal periodicity

There are many scattered observations on seasonal variations of foraging activity in the literature (reviewed by Wood, 1978). The seasonal periodicity is more obvious in areas where the climatic conditions are most variable (Bouillon, 1970). However, a general pattern is sometimes difficult to establish clearly, since activity fluctuates greatly between days. Only continuous observations give the real picture of seasonal activity. This conditions, rarely fulfilled, could explain some of the contradictory conclusions found in the literature.

An explanation of seasonal variation in foraging was sought in climatic factors (mainly temperature and rainfall). Bodot (1967), in studying the foraging activity of *Macrotermes bellicosus*, found a positive relationship with the maximum temperature of the 24 h before, with the mean temperature and with the range of relative humidity ; and a negative relationship (though not significant) with rainfall and the number of rainy days.

Detailed work has been done during 3 years (1976-1978) in Kenya, on foraging activities of *Macrotermes michaelseni* (Lepage, 1979, 1981a & b). The daily activity was monitored over 116 days and was found to be positively related to the maximum temperature of the day before and negatively to the rain of the 5 previous days. The monthly relationship over the 3 years showed that the two factors, temperature and rainfall, could explain 33 % of the foraging activity.

However, the climatic factors alone could not explain all the foraging activity, especially the periods of intense foraging when internal factors depending on the internal economy of the termite colony are preponderant. Swarming lowered the foraging activity. But the main explanation concerning where the maximum foraging activity took place in all the *Macrotermes* species, is the maturation of the sexual brood within the nest. Foraging is clearly a response to increasing needs of the colony.

From the results obtained in Kenya on *M. michaelseni* (Darlington, 1977, 1982a ; Lepage, 1977, 1979, 1981a & b), there was a relatively good agreement ($P < 0.05$) between the foraging activity on the ground (expressed as the number of foraging holes open) and the food balance of the colony (expressed as the ratio fungus-combs weight versus population biomass).

From the figures given by Bodot (1967), it is possible to establish a negative relationship between the food availability (ratio fungus-combs weight to queen weight) and the intensity of the recent foraging activity (ratio of fresh to old fungus-comb). This could explain the constant adjustment of the foraging to the needs of the colony. As a matter of fact, as quoted by Darlington (pers. comm.), though the total weight of the reproductive brood within the nest of *M. michaelseni* varied widely throughout the year, the quantities of fungus-combs showed less variations than expected : it is postulated a feed-back mechanism which constantly adjust the food collected to the consumption by the population. In the other hand, Darlington (pers. comm.) found good correlations between fungus-combs weight and all population parameters (including queen's weight).

Figure 1 brings together four seasonal foraging cycles of *Macrotermes* spp. in different ecosystems, from the data of Lepage (1974a), Wood & al. (1977), Lepage (1981a) and Bodot (1967). The monthly rainfall and the sexual brood maturation within the nests and the swarming time are plotted

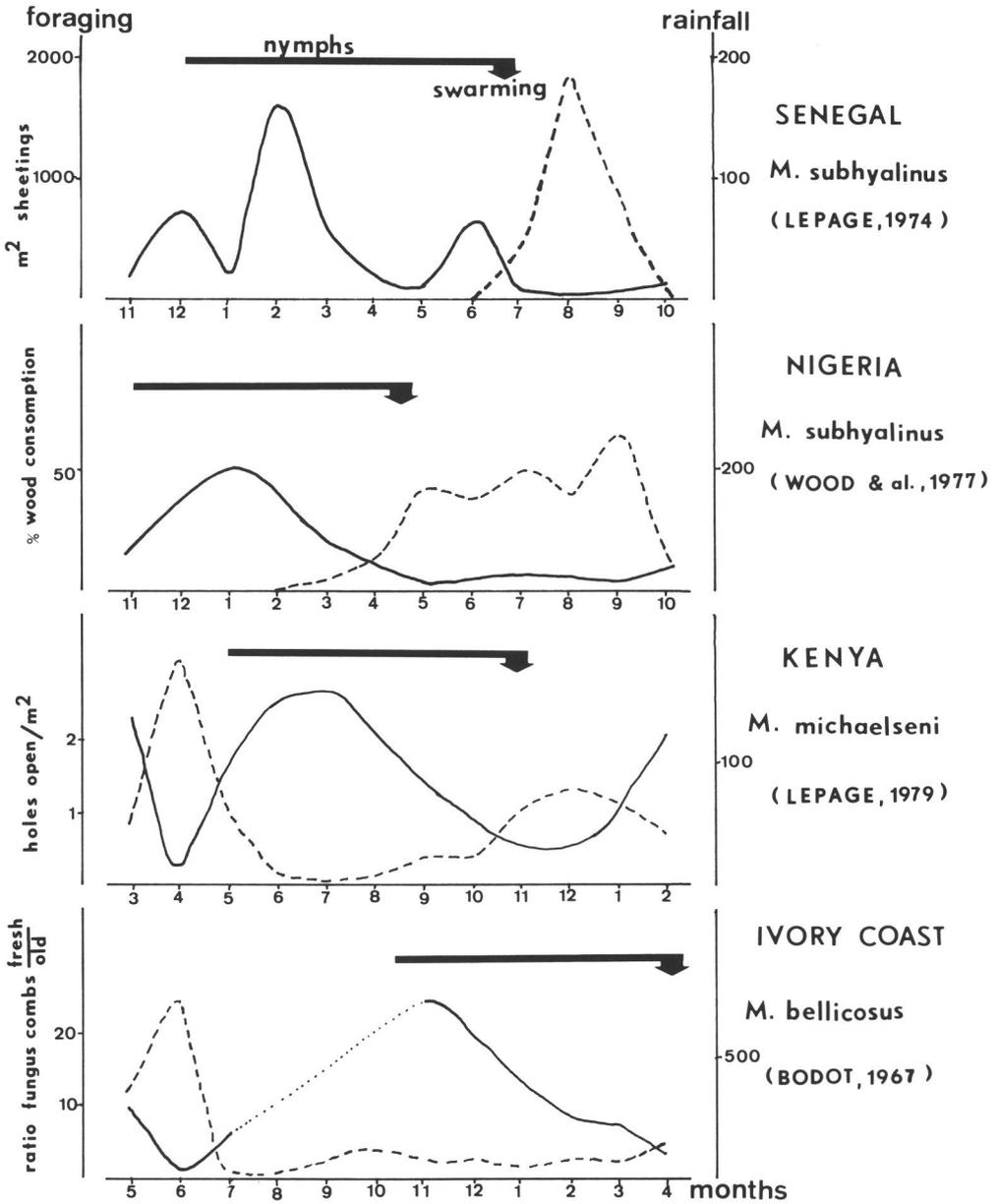


Fig. 1 - *Macrotermes* spp. foraging cycles in four savanna ecosystems (continuous line : foraging cycles ; dashed line : monthly rainfall).

Fig. 1 - Cycles d'approvisionnement de *Macrotermes* spp. dans 4 écosystèmes de savane (ligne continue : cycle d'approvisionnement ; ligne pointillée : précipitations mensuelles).

on the same figure. For all the species studied, the peak of foraging occurred during the first third of the nymphs' development, and the maximum food availability within the nest appeared probably one or two months later.

Since the swarming in all the species studied took place at the beginning of the rainy season, the nymphs' development (5 - 7 months) continued through the dry season, and therefore the peak of foraging activity is located in the dry season. The maturation of nymphs during the dry season in seasonal environments is essential for the successful foundation of new colonies in the rainy season.

DISCUSSION

The success of the Macrotermitinae, and especially the *Macrotermes* species in tropical ecosystems, can be partly explained by their foraging strategies. The fungus-combs are probably a buffering mechanism within the termite colony. Besides their role in degrading plant material, the combs are certainly used as food reserves consumed in periods of starvation. Wood & Johnson (1978) showed that in cultivated ecosystems, *Microtermes* spp. rely on combs during the dry season, resulting in a 50 % reduction in total weight of these reserves in 1-year maize, or in an almost total consumption in a 8-years cultivated field. The high energy demand of the sexual brood, particularly important in the Macrotermitinae, can only be met thanks to the combs reserves during the dry season.

Macrotermitinae are «r» strategists, at least as far as their production of sexuals is concerned : these reproductives sometimes represent more than half of the colony biomass. From the few data available, it seems that an increasing proportion of the budget is devoted to reproduction as the environment become more unpredictable.

Being «r» strategists and ultrageneralists, the Macrotermitinae have all the characteristic features of colonial species and are well adapted to new and fluctuating ecosystems of the tropical zone.

ACKNOWLEDGMENTS. — Some of the personal results accounted for in this work were supported in Sénégal by the International Biological Programme (French) and in Kenya by the International Centre of Insect Physiology and Ecology (French founding).

Dr J.P.E.C. Darlington kindly read and commented upon the manuscript and her help is gratefully acknowledged.

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