

REPRODUCTIVE MECHANISMS IN A *NASUTITERMES* SPECIES (ISOPTERA: TERMITIDAE)

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ABSTRACT

The number of reproductive individuals present in colonies of *Nasutitermes* sp. was analysed, and its possible reproductive strategy discussed. Twenty-four nests were collected and opened, and a single queen and king were found in 17 of them. In the other 7 nests, no queen or king were neither found, nor any other reproductive individual. All queens were weighed, and the number of eggs laid by them was counted. No relationship between the volume of the nests and the weight of their respective queens was found, but the number of eggs laid by the queens during an hour was positively correlated to their weight.

Key words: *Nasutitermes*, Isoptera, Termitidae, reproduction, polygyny.

RESUMO

Mecanismo reprodutivo em *Nasutitermes* sp. (Isoptera: Termitidae)

Foi analisado o número de reprodutores presentes nas colônias de *Nasutitermes* sp., discutindo suas possíveis estratégias reprodutivas. Vinte e quatro ninhos de *Nasutitermes* sp. foram coletados e abertos sendo encontrado uma única rainha e um rei em 17 deles. Nos outros 7, o casal real não foi encontrado e também nenhum outro tipo de reprodutores. Todas as rainhas foram pesadas, sendo contado o número de ovos postos por elas num período de uma hora. Nenhuma relação entre o volume das colônias e o peso de suas respectivas rainhas foi encontrada mas, as análises indicam uma correlação positiva e significativa entre o número de ovos postos por elas durante uma hora e seus pesos.

Palavras-chave: *Nasutitermes*, Isoptera, Termitidae, reprodução, poliginia.

INTRODUCTION

Colonies of termites have an exceptional number of sterile individuals, the workers and soldiers, that are responsible for purveyance and defence of the nest, and by one or more fertile females, the queens, which allocate all their time and energy in reproduction (Thorne, 1984).

Social behaviour allows colonies to overcome morphological, physiological, and neurological limits in relation to solitary species. Reproductive specialisation of queens, coupled with the ability

of the colony to replace dead or senescent reproductive, enable insect societies to function as perennials, while the majority of solitary insects are confined to an annual life cycle (Thorne, 1985). According to Roisin (1987), the number of fertile females involved in egg-laying activities is an important characteristic, owing to their implications in the evolution of sociality. In wasps polygyny, a condition where several impregnated females coexist in a colony, is a situation probably found in primitive social species (West-Eberhard, 1978). The majority of species of ants, bees and termi-

tes has a single queen in their colonies (Wilson, 1971). According to Thorne (1982a), polygyny in Termitidae seems to be a derived condition, being a mechanism by which their societies avoid the ecological and evolutionary restrictions commonly faced by species that are monogynous.

Polygyny in eusocial Hymenoptera as well as in Isoptera may be attained through three possible processes (Thorne, 1985): 1- by differentiation of sexual individuals in satellite nests derived from the original colony; 2- through addition or replacement of the queens by their daughters; 3- by pleometrosis, polygynous foundation of the colony after the nuptial flight.

According to Thorne (1982b), the discussion about multiple queens in Isoptera is complicated by the fact that several types of queens exist within the order. The first type of reproductive would be the primary, that is, queens and kings originated from alates, with wings totally formed and that went through all the pre-reproductive moults. Alates can flight, mate, and find their own nests. In some species they may remain within the natal nest and take over the reproductive position from dead or senescent parents. In this case, reproductives are regarded as adultoid (Noirot, 1969). The second type would be the brachypterous neotenic (or nymphoids) reproductives that develop along the same nymphal pathway as the primary forms, but that at the final moult do not develop membranous wings. This type stays within the natal colony, and females do not become quite as large as primary queens. The third type corresponds to apterous neotenic or ergatoid reproductives, that originate from larvae or from pseudergates in lower termites, or workers in higher termites (Thorne, 1982b; Darlington *et al.*, 1992).

The ecological success of an Isoptera colony is influenced by the reproductive capacity of the queens. Among the different strategies developed by the termites, the capacity of replacing reproductives seems to be of great importance. As noted, their societies are headed by a pair of dealate imagoes which have found the colony soon after an alate flight. After the death of these reproductives, the colony only survives if replacement reproductives are developed (Lefeuvre, 1987). Until the seventies, replacement of the original reproductives was known to occur frequently within the Kalotermitidae (Miller, 1969), but no cases

were reported for Termitidae (Noirot, 1969). However, after the seminal studies of Thorne (1985), it has become evident that the occurrence replacement of reproductives within the Termitidae was not uncommon.

In the family Termitidae, adultoid, nymphoid and ergatoid reproductives can be found (Noirot, 1969) and, according to Lefeuvre (1987), these three types of reproductives may be present in colonies of different species of *Nasutitermes*. Ergatoid reproductives can be differentiated in *Nasutitermes novarumhebridarum* N & K. Holmgren (Roisin, 1987) and in *Nasutitermes columbicus* Holmgren (Thorne & Noirot, 1982). In *Nasutitermes princeps* Desneux, all the replacement queens and kings are ergatoid (Roisin & Pasteels, 1986a). In general, the reproductive pattern is highly complex within the Termitidae, because a single species may adopt different reproductive strategies (Roisin & Pasteels, 1985).

The objective of the present study was to verify the number of reproductives present in colonies of *Nasutitermes* sp., and to discuss their possible reproductive strategies.

MATERIAL AND METHODS

Mounds sampled in this study were located at a Cerrado area in the Municipality of Itirapina, São Paulo, Brazil (22°15'S and 47°49'W, altitude of 765 meters).

The study area is an alluvial plain covered by a sandy sediment, with a deep, quartzes' sand soil type (Oliveira & Prado, 1984).

Mean annual rainfall is 1,425 mm, with the rain season extending from October to March, when 84% (1,199 mm) of the precipitation occurs. The most rainy months are December, January and February, with precipitation average values equals to 288, 266 and 262 mm, respectively. The driest months are July and August, with 16 and 19 mm of precipitation, respectively. The mean annual temperature is 19.7°C, with January and February being the hottest months with respective mean values of 22.2 and 22.3°C. The coldest months are June and July with respective mean temperatures of 16.4 and 16.2°C.

Due to the difficulties in studying the Isoptera mainly the genus *Nasutitermes*, the species studied in this paper was just identified till genus even after

enquiries to Brazilian and foreign taxonomists (Dr. Reginaldo Constantino – University of Brasilia – Brazil and Dr. Kumar Krishna – New York Natural History Museum). In face of this, we deposited reference specimens in the Museu de Zoologia da USP (MZUSP 9921) at São Paulo state capital city.

Twenty-four nests were collected and their diameters and heights measured. To calculate nest volumes, it was assumed that the nests had an approximately spherical calotte form (Fig. 1) so that the following formula was used:

$$V = \frac{\pi}{6} \times h(3r^2 + h^2),$$

where r = the radius and h = the height of the nest. Since no descriptions of the nests of this species are available, all nests were transferred

to the laboratory and completely dissected because the reproductives are difficult to locate. Once they were found, reproductives of the 12 nests out of the 24 collected were weighed (wet weight) with a precision balance.

To measure the rate of egg-laying by the queens, each queen was placed, after being weighed, together with the king (when found) and with 10 workers, in a Petri dish covered with moist filter paper. They were kept in this condition for 21 to 67 hours. Regressions between the volume of the colonies and the weight of their respective queens, and between the number of eggs laid by the queens during an hour and their respective weights were carried out.

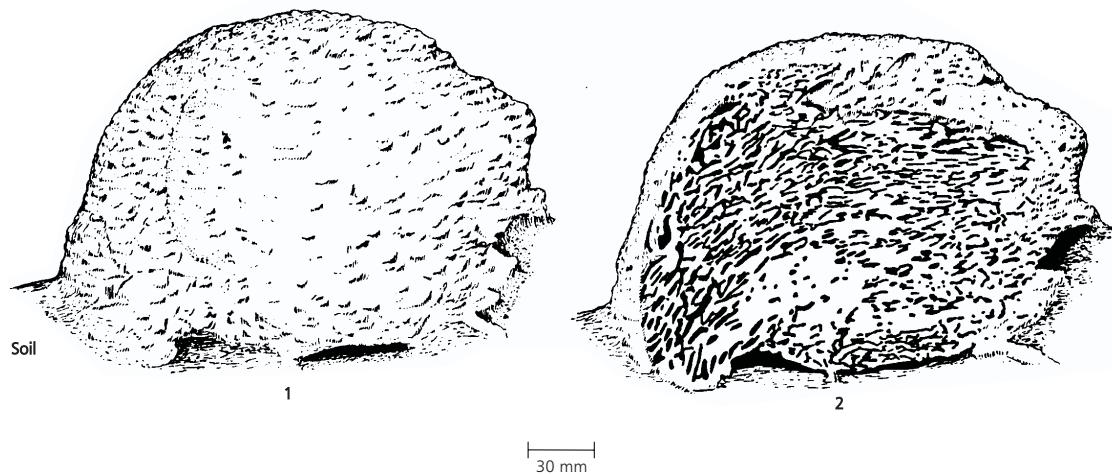


Fig. 1 — External (1) and internal (2) view of a *Nasutitermes* sp. mound.

RESULTS

In 7 out of the 24 sampled nests, no queens or kings were found, nor any other type of reproductives, independent of the presence or not of eggs and/or juveniles individuals. According to own observations the polycalism did not exist in *Nasutitermes* sp.

In 17 nests a single physogastric queen was found. However, the weight of some of them was not recorded because the queen was damaged while the nests was opened. Mean weight of the queens

was 0.0714 grams ($n = 12$; $s = 0.025$). A single king was found with each queen, with a mean weight of 0.0115 grams ($n = 10$; $s = 0,002$) (Table 1).

There was no significant regression between the volume of the nests (V) and the weight (W) of their queens: $V = 6.009 + 74.298W$ ($r = 0.052$; $n = 12$; $P = 0.475$; Fig. 2). A strongly positive relationship between the number of eggs laid in an hour (N) and the weight of these queens (W) was found: $N = -14.945 + 351.577W$ ($r = 0.833$; $n = 10$; $P < 0.000$; Fig. 3).

TABLE 1
Nest volume, queen and king weights and number of eggs laid by queens during an hour period for *Nasutitermes* sp.

Nest number	Queen weight (g)	King weight (g)	Number of eggs/hour	Nest volume
1	0.044	0.014	0.448	22.55
2	0.061	0.009	1.462	7.49
3	0.076	–	4.417	22.36
4	0.037	0.011	1.317	5.58
5	0.057	0.012	4.208	15.93
6	0.084	0.014	–	7.38
7	0.057	0.011	4.583	3.84
8	0.101	0.012	22.667	8.09
9	0.107	0.012	–	8.51
10	0.065	0.010	10.333	1.93
11	0.054	0.011	8.417	6.65
12	0.113	–	26.956	25.48
\bar{X}	0.071	0.012	8.481	11.32
S	0.025	0.0016	9.196	8.074

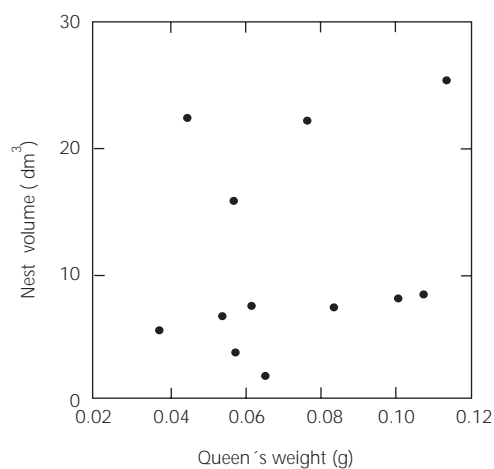


Fig. 2 — Scatter diagram showing the relationship between the volume of a colony and the weight of its queen ($r = 0.052$; $n = 12$).

DISCUSSION

In termites, the loss of reproductives is a disastrous event for their societies, which will die if new sexual individuals do not differentiate (Lefeuve, 1987). Although the study area is continuously disturbed by cattle, and the nests of *Nasutitermes* sp. were predated by armadillos and other vertebrates, the presence of a physogastric queen and a king was always observed.

Lefeuve (1987) verified that the colonies of *Nasutitermes coxipoensis* Holmgren are exclusively monogynous, with a single queen and king being found among them. Even after nests were orphaned, this author was not able to find more than a single queen and king. According to him, in this species, the replacement reproductives are adultoids that probably differentiated outside the period of development brood.

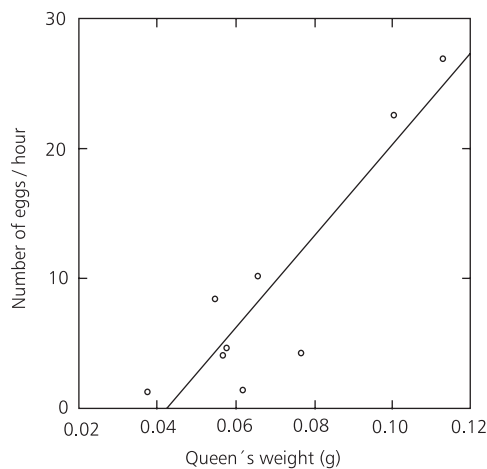


Fig. 3 — Scatter diagram, and regression line, between the number of eggs laid per hour and the queen's weight ($r = 0.052$; $n = 12$).

The replacement queen soon becomes physogastric. Thus, the level of physogastry does not depend only on the age of the queen but also on the sterile population of the colony, a fact corroborated by the present study, where it was found that the queen did not always inhabit the biggest (in terms of volume) nest.

In a study carried out with *Nasutitermes princeps*, Roisin & Pasteels (1986a) suggested that the degree of physogastry reached by the queen depended on the worker caste that maintains it, and that this caste number is inversely proportional to the number of queens that differentiated after the death of the primary reproductives. Thus, in polygynous societies, secondary queens interact to produce eggs at a rate that is equal or higher in comparison with the rate observed in primary, physogastric queens (Thorne, 1982a,b; Roisin & Pasteels, 1986a).

Roisin & Pasteels (1986b) observed that colonies of *Nasutitermes novarumhebridarum* have a single queen, and that orphaning invariably leads to differentiation of ergatoid reproductives. Since these reproductives were only obtained in experimental conditions, they concluded that, in nature, these reproductives were seldom produced and that the sexual individuals encountered were those that founded their colonies. Thus, winged dispersion constituted, in this species, the main, if not the only, way that colonies are founded. Since differentiation of adultoid or nymphoid sexual replacements seem

to be frequent in Termitidae (Thorne, 1985), Roisin & Pasteels (1986b) challenged the apparent incapacity of young sexual individuals of *Nasutitermes novarumhebridarum* to produce such reproductives once the primary queen is lost. For Roisin & Pasteels (1986b), it is possible that the selective pressure favouring the replacement of queens in this species is weak. Moreover, it seems that its colonies are found in sites where food is abundant, but not always available, and disperse, so that the loss of the primary queen is associated with the depletion of the resource of the society. In this situation, it will be more "advantageous" for the winged individuals to disperse rather than become reproductives in its colonies. This rigidity in the nymph development may secure to the society a total investment in the winged dispersion. On the other hand, workers that might differentiate into ergatoid reproductives will not have anything to lose in trying to continue reproduction in their colony.

In *Nasutitermes polygynus* Roisin & Pasteels and *Nasutitermes princeps*, the development of nymphs and imagoes is more flexible, with their colonies often polygynous. Formation of replacement reproductives and multiplication of the colony by "budding" has an important role in the reproductive biology of these species, since these strategies are linked to the longevity of the society and to their expansion capacity (Roisin & Pasteels, 1986b). Replacement of reproductives

in *Nasutitermes princeps*, leading to polygynous societies, may be a natural event in the colony, independently of any accident (Roisin & Pasteels, 1986a).

According to Thorne (1984), prevalence of polygyny in a population probably depends on age, on the history of each colony and on biotic as well as abiotic factors. Multiple queens are commonly found in young colonies located in habitats with enough resource to allow its rapid increase, or in habitats where predation and/or competition pressure is strong enough, with colonies having great reproductive and survival advantages.

An ecological advantage of polygyny in incipient colonies is given by the increase in the numbers of eggs produced and, hence, in the expansion of the population within the colony, at least in habitats with an adequate food supply. Such expansion results from the substantial increase of the sterile population, which is pivotal for the growth of the colony in this stage, since workers are necessary for nest building, brood care and foraging, and soldiers are necessary for defence. Thus, colonies with two or more reproductive females have high rates of survival during the vulnerable period, simply because the nest grows faster during this stage. Thorne (1982b) argued that polygynous colonies of *Nasutitermes corniger* reach a threshold in the sterile population and, hence, a considerable size, before the production of winged individuals. According to her, this also anticipates the production of reproductives, with the first generation of these individuals being produced earlier than in monogynous colonies, having, as a corollary, a distinct advantage in terms of Darwinian fitness (Cole, 1954 *apud* Thorne, 1982b).

From what has been discussed up to now, and taking in consideration the factors that could lead to the production of secondary reproductives in termites, one can think that in *Nasutitermes* sp. a strategy similar to that used by *Nasutitermes coxipoensis* (Lefeuvre, 1987) is being employed, with differentiation of a single queen and king, with their colonies being monogynous. The substitute queen quickly would become functional, so minimizing damage and risks to the colony, but this possibility is small when considering that during one year the growth rate of the colonies was null (Buschini, 1996).

Thus is possible that its reproductive strategy is like that of *Nasutitermes novarumhebridarum* (Roisin & Pasteels, 1986b). Considering that the aggregation pattern of their colonies is regular, suggesting competition between them (Buschini, 1996), it is possible that, under these conditions, the selective pressures from predators such as armadillos, ants and rodents may have not being strong enough to promote differentiation of secondary reproductives, since resource availability seems to be limited. The high aggressiveness observed between individuals from different colonies (Buschini, 1996) suggest that they possess well defined territories. Abe & Darlington (1985) concluded that the nests of termites tend to a regular distribution due to territoriality, with their densities being limited by competition between colonies for food and/or nesting areas and by predation pressures. According to them, this happens in the early stages of the development of a colony. If so, then, how colonies of *Nasutitermes* sp. could adopted such reproductive strategy, since the chances of increasing their foraging territories and of settling new colonies in this area are, probably, small? Is it not more advantageous, under the conditions that this species encounters, to produce and disperse winged individuals for colonisation of new areas where resources are more abundant?

The results gathered in this study do not rule out the possibility that this species may have polygynous colonies, at least in circumstances different for those hitherto found. For example, early in the colonisation of this area, with the resources being more abundant, selective pressure from predators may be strong enough to lead them to adopt such a reproductive strategy, since the number of nests attacked by predators is high. This may be, also, one of the explanations for the great size difference between some of its colonies, considering that the biggest volume found was equal to 192.46 dm³, that 70.5% of all nests sampled had volumes lower than the mean value (16.31 dm³), and that only 9% of the colonies showed volume above 70 dm³ (Buschini, 1996). Thus, as resources become scarce, it may be that the reproductive strategy of this species changes, with colonies becoming a monogynous. According to Thorne (1984) a single species may show different frequencies of colonies with multiple queens, depending on the site where it is found.

She noted that all the colonies of *Nasutitermes corniger* Motschulsky collected in areas of secondary growth in Panama, with a high vegetative production, high number of young colonies, high turnover of nesting sites and mild predation pressures, showed high frequencies of polygyny. This frequency decreases if sampling is taken in a nearby primary forest.

Another possibility is that the colonies of *Nasutitermes* sp. were founded by more than one female (pleometrosis) or by a single queen and king. Roisin & Pasteels (1985) showed that polygynous societies of *Nasutitermes princeps* reached sizes well above those reached by monogynous colonies. Thorne (1985) suggested that polygyny in *Nasutitermes corniger* and *Macrotermes michaelseni* Sjöstedt may be formed by pleometrosis, after the nuptial flight.

According to Thorne (1982c), *Nasutitermes corniger* has an exceptional reproductive plasticity that allow its colonies a successful adjustment to several different microhabitats, with varying degrees of disturbance, and a rapid recovery after disturbance. It is possible that the colonies of this species and its queens, in different habitats and with distinct histories, showed different growth rates. In this species, colony foundation may result from cooperation between different females (Thorne, 1982b).

The absence of a correlation between the volume of the colonies and the weight of their respective queens is probably due to the different histories of each colony since the physogastry is not influenced by its age but by the external as well as by the internal (colony) environment, such a high number of sterile individuals, the queen's health, etc. Another explanation may be that, for any reason, a primary queen was replaced by an adultoid reproductive, which can justify its low weight in colonies with a certain degree of development. It is also possible that colonies with more developed queens and, hence, heavier, constitute evidence for the occurrence of accidents, which leads to a delay in its growth rate. In a study of nest growth, it was observed that during a period of an year the growth rate was null, with factors such as the degree of injuries suffered by then invoked as responsible for these results (Buschini, 1996).

As queens grow old, it is expected that they reach a high degree of physogastry, consequently

laying more eggs, increasing the number of individuals and hence the populations and volume of the colonies and nests. Since the frequency of injuries suffered by their nests is high, one expects a decrease in the number of individuals, with an increased necessity to rebuild and reconstruct the harmed structures, which leads to a delay in its development. Taking into account the fact that the physogastry of the queen does not depend only upon its age, but also upon the sterile population that supports it (Lefeuvre, 1987), it is possible that its development becomes slower. But, since it has already attained a certain degree of physogastry, and part of the colony structure was lost, this may constitute one of the reasons for the absence of a correlation between the weight of the queens and volume of the colonies.

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