

DEVELOPMENT OF NESTS AND COMPOSITION OF
COLONIES OF *NASUTITERMES NIGRICEPS*
(ISOPTERA: TERMITIDAE) IN THE
MANGROVES OF JAMAICA

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ABSTRACT

Colonies of *Nasutitermes nigriceps* (Haldeman) inhabiting the island of Jamaica were extracted from their arboreal carton nests by a two-stage method in which the termites were dislodged from their galleries and separated from nest debris by flotation in water. Recovery of termites by this process was 97.7%.

No incipient nests were observed and all small nests collected consisted of both a wooden region, which housed the reproductives, and an external carton nest. Except for the soldier caste, the proportion of sterile castes was similar in both regions of the nest. The size of small nests increased with little changes in the total colony size. However, the number of termites in the external carton nest increased with size of colony.

Approximately 50% of the large nests contained reproductives. These colonies were consistently monogynous and monandrous. Caste composition of *N. nigriceps* colonies was comparable at each sample site and in nests of both reproductive status. However, large nests had a smaller proportion of immature termites, but similar proportion of soldiers. The average percentage of workers in small nests was proportional to that of large nests with reproductives, but less than large nests without reproductives.

Key Words: *Nasutitermes*, termites nest, colony composition.

RESUMEN

Las colonias de *Nasutitermes nigriceps* (Haldeman) que habitan la isla de Jamaica fueron extraídas de sus nidos arbóreos por un método de dos pasos mediante el cual las termitas se separaron de sus galerías y se separaron del ripio usando un método de flotación en agua. El porcentaje de termitas recuperadas fue del 97.7%.

No se observaron nidos incipientes y todos los nidos pequeños consistieron de una parte leñosa, en la cual se encontraron los estados reproductores, y un nido externo de cartón. A excepción de la casta de soldados, la proporción de castas estériles fue similar en ambas partes del nido.

El incremento del tamaño de los nidos pequeños no significó un gran cambio en el tamaño de la colonia.

El 50 % de los nidos grandes contenían estados reproductores. Estas colonias eran consistentemente monoginas y monandras. La composición de ambos estados reproductivos de las colonias de *N. nigriceps* fue comparable en cada sitio muestreado y en cada nido. Sin embargo, nidos grandes tuvieron una proporción menor de estados juveniles de termitas, pero una proporción similar de soldados. El porcentaje promedio de obreras en los nidos pequeños fue proporcional al de los nidos grandes con estados reproductores, pero los nidos pequeños tuvieron un porcentaje menor de obreras que los nidos grandes sin estados reproductores. Las colonias de *Nasutitermes nigriceps* (Haldeman) que habitan la isla de Jamaica fueron extraídas de sus nidos arbóreos por un método de dos pasos mediante el cual las termitas se separaron de sus galerías y se separaron del ripio usando un método de flotación en agua. El porcentaje de termitas recuperadas fue del 97.7%.

The Caribbean island of Jamaica is the third largest in the West Indies and has 16 documented species of termites belonging to the families Kalotermitidae, Rhinotermitidae and Termitidae (Snyder 1956). Advanced species of the family Termitidae are represented by *Termes hispaniolae* (Banks), *Nasutitermes nigriceps* (Haldeman), *Nasutitermes costalis* (Holmgren), *Nasutitermes hubbardi* Banks. *N. nigriceps* is the most common and prominent species of arboreal termite on the island with populations distributed in both natural forests and human-developed habitats.

Advanced species of termites enhance their survival by evolving specialized castes protected in tough and complex nests. Previous studies of the composition of *Nasutitermes* colonies have been documented in *N. rippertii* (Rambur) (Krecek 1970), *N. costalis* (Krecek 1970, Clarke 1990), *N. corniger* (Motschulsky) and *N. ephratae* (Holmgren) (Thorne 1985), *N. exitiosus* (Hill) (Watson & Abbey 1987). Unfortunately, the data are not comparable because of differences in extraction methods and accuracy of results. The problem of ascertaining the composition and size of *N. nigriceps* colonies was surmounted in this study by the use of a simple and replicative extraction process, which yields almost full recovery of termites in nests. The density of nests and growth pattern of colonies, including the proportion of castes at various stages of development, were examined.

MATERIALS AND METHODS

The study focused on populations of *N. nigriceps* inhabiting mangrove forests because this environment offered virtually undisturbed, accessible nests that could provide an accurate description of colony and nest development. The three study sites selected were Port Royal, Hellshire and the North Coast. Four species of mangroves occurred in these areas. In order of abundance these are *Rhizophora mangle* L. (red mangrove), *Avicennia germinans* L. (black mangrove), *Laguncularia racemosa* Gaertn (white mangrove) and *Conocarpus erectus* L. (buttonwood mangrove). Before assessment of colonies commenced, the density of nests at each site was determined by counting the number of live nests in 6 randomly chosen 30 m x 30 m quadrats. Viability of nests was visibly assessed by creating holes in the upper, mid and lower regions of nests and observing the emergence or non-emergence of termites.

Between June 1987 and May 1988, five nests per month were randomly selected from each site. Each nest was half an ellipsoid in shape (Fig. 1) and the longest perimeter, height and diameter of base were measured before removal of nest from the supporting branch. These measurements were used to calculate the volume of the nest. Both the carton and wooden sections of small nests were removed for analysis, while those nests consisting solely of a carton structure were dislodged from the supporting branch by repeatedly hitting the branch with a hatchet. Each nest was placed in a plastic bag and transported to the laboratory where it was first subdivided and fumigated with carbon dioxide in reinforced plastic bags for 10-15 min. During stage one of the extraction process each piece of subdivided nest was further broken into small pieces and shaken by hand to dislodge the termites from the galleries. The termites and nest debris resulting from shaking all the pieces of a whole nest were collected in a tray and the empty pieces of nest from which the termites had been removed were discarded.

Termites were separated from the nest debris during stage two of the extraction process by flotation in water. The total mixture of termites and nest debris derived from a single nest was submerged in water and allowed to stand for approximately 30 min. The nest material rapidly becomes saturated and sinks; then the floating termites can be easily removed. For a clearer separation, small volumes of the total suspension were successively removed, stirred in water and allowed to stand for 10 min. The water with the floating termites was decanted into a double sieve with upper and lower mesh sizes of 0.05 mm and 0.025 mm, respectively. The remaining debris

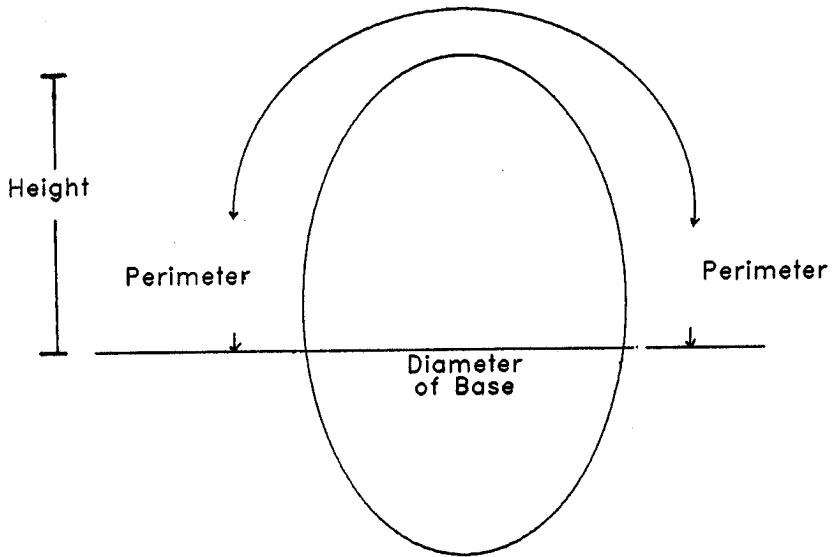


Fig. 1. Structure of nest.

in the bucket was rewashed with water to ensure complete removal of termites. The water was drained from the termites and the total amount of termites measured. Three sub-samples of 5 ml each were removed and the number of each caste counted. The total colony size and caste composition were calculated.

The efficiency of the two-stage extraction method was determined by processing 10 nests and assessing the amount of termites remaining in a) the pieces of nests to be discarded after shaking the termites from the galleries and b) the waste residue in the bucket after flotation. Unlike the powdery residue in the bucket after stage two, the pieces of nests to be discarded after shaking were crumbled before flotation. Complete retrieval of termites was determined by visual observation.

The mean percentages and standard deviation of sterile castes were calculated from Arcsine transformed data (Sokal & Rohlf 1981, Zar 1984). Only re-transformed data are quoted in this paper; consequently, for some results the total percentage of castes per nest are not equal to 100. Analysis of variance and Student's "t" test were used for comparisons of means.

RESULTS

The density of *N. nigriceps* nests varied in each sample site (Table 1). Port Royal mangroves supported the highest number of live termite nests and, contrary to the other sites, some nests were situated in proximity to each other. Consequently, during the monthly sampling, the number of nests collected from Port Royal was significantly greater than Hellshire and the North Coast. Incipient nests were not observed at the three sites and only a few small nests ($N = 12$) were found in the mangroves of Port Royal. These small nests occurred in proximity to each other while larger nests were widely separated (Fig. 2; Spearman Rank test $r = -0.8$, $P > 0.05$). Each small nest consisted of an interconnecting wooden and an external carton nest. The wooden nest was ramified with galleries and some areas were lined with

TABLE 1. DENSITY OF NESTS IN THE THREE STUDY SITES.

Quadrat	No. of Live Nests ¹		
	Port Royal	Hellshire	North Coast
1	0 (1)	0 (1)	1
2	2 (1)	1	0 (1)
3	3	0 (1)	1
4	2	0 (1)	1
5	5	1	1
6	3 (1)	1	1
x	2	0.5	1

¹() No. of dead nests.

stercoral carton. The perimeter of the friable, external carton nest ranged from 10-35 cm. The number of termites in the external carton nest increased with colony size (Fig. 3). Large nests with perimeters 34-130 cm (N = 101) consisted solely of an external carton nest. The colony size of these large nests increased proportionally with nest size ($r = 0.5, P > 0.001$), while in smaller nests there was an increase in the size of nests with no corresponding increase in the number of termites (Fig. 4).

N. nigriceps nests were enlarged during the island's bimodal rainy season that peaks in May and October. The direction of growth of small nests was multilateral, but mainly negatively geotropic in large nests. The latter pattern of nest expansion was consistent in large nests that had fallen from branches. The lower and older region of large nests with perimeter greater than 87 cm were devoid of termites. The

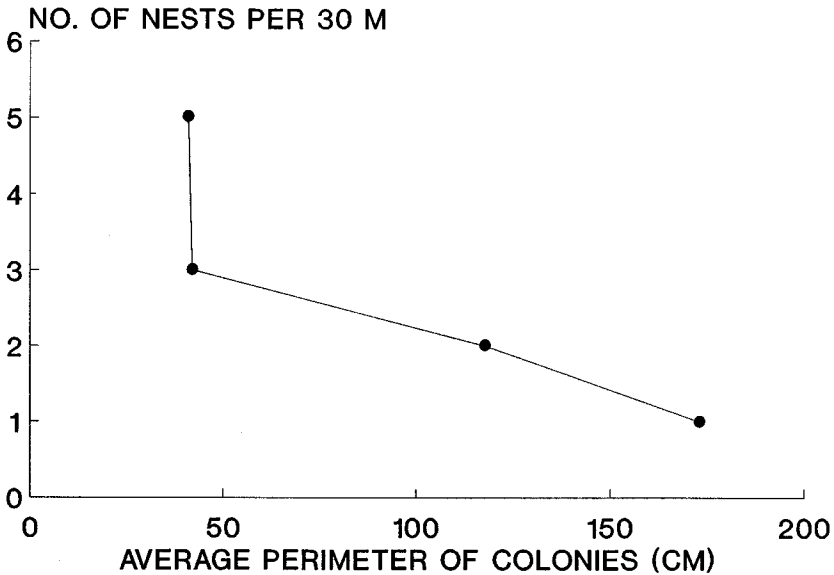


Fig. 2. The relationship between the density (No. per 30m²) and perimeter of nests.

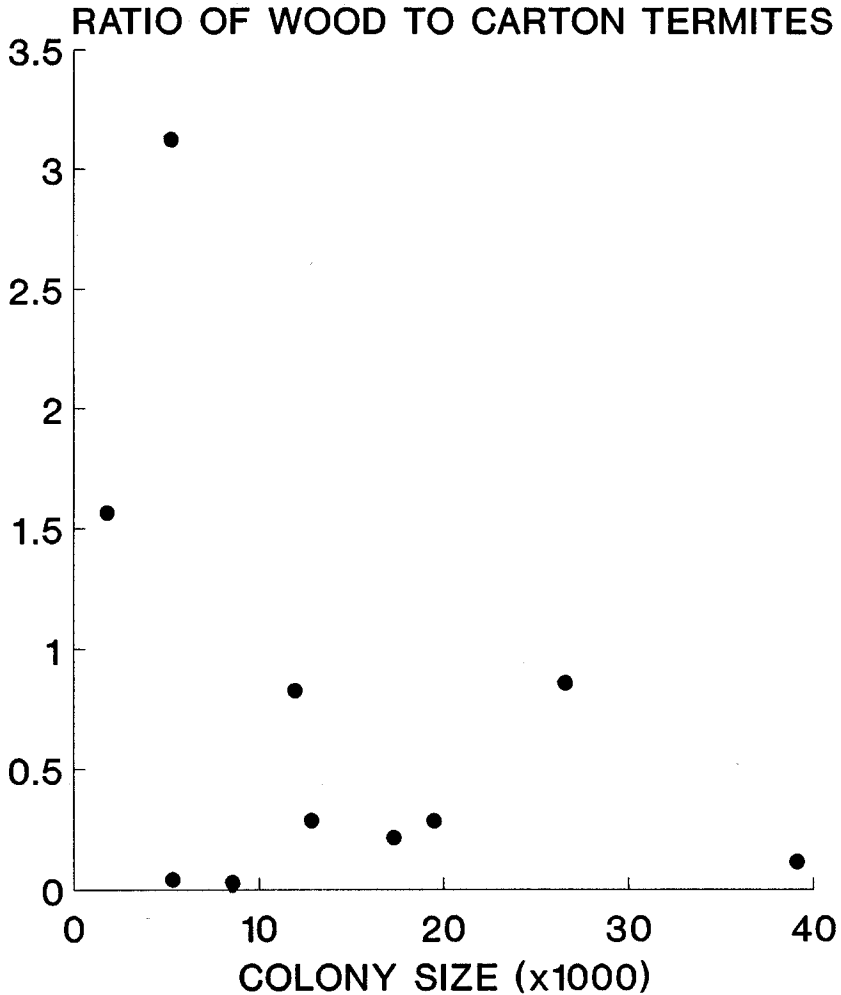


Fig. 3. The effect of colony growth on the distribution of termites in the wooden and carton regions of nests.

walls were paler in color and separated easily between the fingers. These vacant galleries were invaded by inquilines.

The shaking-flotation extraction method produced a clean sample of sterile termites devoid of nest debris. The mean number of termites per 5 ml ranged from 941-1195 (Table 2). The average recovery of termites by shaking and flotation was 98.3% and 97.6%, respectively (Table 2). Total recovery of termites utilizing the two-stage method was 97.7%. Colonies of *N. nigriceps* consisted of the typical castes found in termite societies. All small nests contained a pair of reproductives in the wooden nest region. Approximately half of the large nests had a pair of reproductives protected by a fortified royal chamber embedded within the core of the nest. The remaining nests of similar sizes did not have reproductives and no royal chambers were found. Imma-

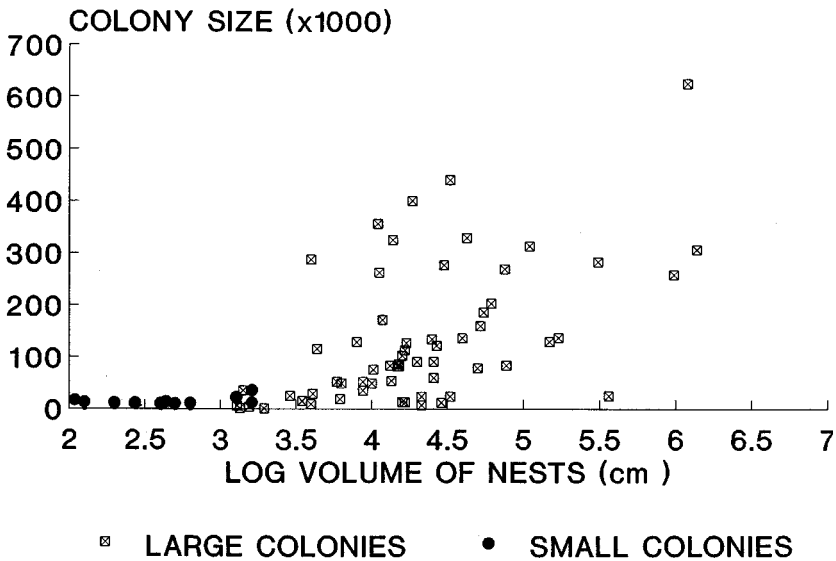


Fig. 4. The relationship between the size of colonies and volume of nests.

ture termites and workers of small nests were equally distributed in the wooden and carton regions (Table 3; $P > 0.05$), while soldiers occurred in large proportions in the carton nest ($P < 0.01$). Although the proportion of sterile castes was highly varied in

TABLE 2. RECOVERY OF *N. NIGRICEPS* FROM NESTS USING A TWO-STAGE EXTRACTION METHOD.

Nest No.	Percentage of Termites Recovered			Mean No. of Termites per 5ml
	Shaking	Washing	Total	
1	97.2	93.7	95.5	1 195
2	99.2	98.6	98.9	964
3	99.0	91.3	95.2	1 066
4	98.5	95.8	97.2	1 046
5	98.6	98.6	98.6	941
6	92.2	98.5	95.4	987
7	92.6	97.4	95.0	1 083
8	99.1	98.9	99.0	1 034
9	98.8	99.3	99.1	1 001
10	99.9	99.2	99.6	1 146
Mean ¹	98.3	97.6	97.7	
SD (min, max)	2.9, 1.5	2.9, 1.7	2.2, 1.5	

¹X and SD were calculated from Arcsine transformed data.

TABLE 3. THE MEAN PERCENTAGE (CALCULATED FROM ARCSINE TRANSFORMED DATA) OF CASTES IN TWELVE SMALL NESTS OF *N. NIGRICEPS*.

Castes	Section of Nest ¹	
	Wooden Region	Carton Region
Larvae	20.9 (8.1; 37.9)	21.0 (4.7; 44.7)
Presoldiers	1.3 (0.4; 2.7)	1.2 (0.3; 2.6)
Soldiers	12.4 (7.6; 18.1)	17.1 (5.9; 32.4)
Workers	63.3 (45.1; 79.9)	55.2 (45.1; 79.7)

¹Minimum and maximum SD in ().

large nests, the composition of castes was not influenced by geographical location and presence of reproductives (Table 4). Small nests from Port Royal had a higher percentage of larvae and presoldiers (immature individuals) than large nests ($P < 0.01$). The proportion of workers in small nests was similar to that of large nests with reproductives ($P < 0.01$) but less than that of large nests without reproductives ($P > 0.05$). Soldiers were equally represented in colonies at different stages of nest development and reproductive status.

DISCUSSION

A *N. nigriceps* colony is initiated in a tree cavity by alates, and wooden galleries are created to house the expanding colony. At a later stage of nest development an external carton nest is built with walls composed primarily of stercoral material (partially digested wood). Initially, the nest material is malleable, but hardens with age. Very little information is known about the dynamics of incipient colonies in the field because of the clandestine nature of the termites and the absence of detectable external diagnostic features of nests. However, *N. nigriceps* colonies inhabiting small nests with both wooden and external carton regions, increased carton nest space

TABLE 4. THE MEAN PERCENTAGES (CALCULATED FROM ARCSINE TRANSFORMED DATA) OF CASTES IN LARGE NESTS OF *N. NIGRICEPS*.

Castes	Sites ¹		
	Port Royal	Hellshire	N.W. Coast
<u>Reproductives Present</u>			
Larvae	18.8 (11.1,25.9)	20.6 (16.6,25.5)	19.5 (19.4,19.6)
Presoldiers	1.8 (0.6,3.7)	1.6 (1.6,25.5)	1.1 (0.9,1.6)
Soldiers	14.5 (10.1,43.7)	14.5 (11.3,18.0)	13.7 (10.5,16.9)
Workers	80.7 (53.7,73.9)	78.8 (56.7,68.6)	82.4 (59.3,71.1)
N	30	8	8
<u>Reproductives Absent</u>			
Larvae	16.8 (9.5,27.6)	23.7 (13.1,36.6)	33.4 (9.3,36.2)
Presoldiers	1.7 (0.4,3.3)	1.4 (0.3,3.0)	1.3 (0.0,2.0)
Soldiers	13.1 (9.1,14.3)	13.6 (10.2,17.0)	13.1 (10.7,17.3)
Workers	84.7 (55.9,78.0)	75.5 (49.1; 71.4)	76.4 (49.5;72.3)
	30	12	13

¹Minimum and maximum SD in ().

with limited increase in total colony size. Such activity not only allows rapid development of a nest that offers better protection from biotic and abiotic factors, but also creates an environment with a more stable and optimum micro-climate. The original wooden nest is abandoned and the colony continues development in the carton nest. Colony composition of *N. nigriceps* varies with the stage of nest development. However, the proportion of each caste seems to stabilize in large colonies at different locations and is not influenced by proportional increase in colony and nest size. Thus, the data presented in this paper may be applied to populations throughout Jamaica.

Mature colonies accommodate the increasing numbers of termites by seasonal expansion of nests. During the rainy season, *N. nigriceps* workers build in a negative geotropic direction. Migration of termites within nests also follow a similar pattern so that termites are continuously associated with fairly new stercoral walls. This inter-relationship may be linked to the homeostatic properties of stercoral material. A review of Noirot (1970) showed the positive influence of stercoral walls on temperature and humidity within nests. The homeostatic nature of stercoral walls of *N. nigriceps* nests may decline with age as seen in its physical parameters such as texture and color. Further research is required for confirmation.

N. nigriceps colonies with reproductives were consistently monogynous and monandrous, but approximately half the nests were devoid of reproductives. The latter may be either calies (subsidiary nests) or large nests which lost their reproductives. Similarity in size of both types of nests, comparable caste composition, absence of a royal chamber in queenless nests and distance between nests, suggest that these large nests without reproductives are calies. Calies have never been recorded in *N. nigriceps*, but were documented in some members of the genus; *N. corniger* (Thorne 1982), *N. costalis* and *N. polygynous* (Roisin and Pasteels 1986). While it is still not clear what induces the development of calies, it has been suggested that they are constructed in response to adverse conditions created by increase colony size (Holt & Easey 1985; Adams & Levings 1987).

A hardened nest inhabited by a large colony hinders accurate determination of the size and composition of the colony. The use of shaking and flotation as methods of collecting insects is not a novelty (Southwood 1978), however, the two-stage method described here has never been utilized to extract termites of the genus *Nasutitermes*. This method is comparable with that used by Darlington (1984) and Thorne (1985). Thorne (1985) removed *N. corniger* and *N. ephratae* (after inactivation by freezing) by a similar shaking method, but the termites were not separated from the nest debris before subsampling thus, resulting in a variation of 400-900 termites per 5 ml subsample. This highlighted the need for a second stage in the extraction method that would provide a cleaner separation and ultimately increase precision. Darlington's (1984) study of *Macrotermes* spp. found flotation useful in separating termites from the rubble generated from the dissection of their huge nests, hence developed a special flotation tank. The two stage method used in this study allows rapid collection of accurate data with the use of simple equipment such as buckets, trays and a portable 10 lb cylinder of carbon dioxide.

ACKNOWLEDGMENTS

The research was funded by The University of the West Indies. We thank Dionne Miller and Johanna P.E.C. Darlington for useful discussions.

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