# ARCHITECTURE AND NUTRIENT ANALYSIS OF ARBOREAL CARTON NESTS OF TWO NEOTROPICAL *NASUTITERMES* SPECIES (ISOPTERA: TERMITIDAE), WITH NOTES ON EMBEDDED NODULES

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## ABSTRACT

Nest architecture of the arboreal Neotropical termites *Nasutitermes acajutlae* (Holmgren) and *N. nigriceps* (Haldeman) is described, with special reference to carton inclusions or nodules found within the normal gallery matrix of some nests. Nutrient analyses of these nodules show that they have high cellulose and low cutin concentrations in comparison to normal nest carton. These data support the hypothesis that the nodule inclusions serve as a form of facultative food storage in some nests of these termite species. These cases appear to represent a rare situation in which food is not stockpiled or cultured by termites, but rather some partially processed, masticated food is incorporated into the nest matrix for future consumption.

Key Words: Termites, Nasutitermitinae, inclusions, food storage.

## RESUMEN

Se describe la arquitectura del nido de las termitas neotropicales *Nasutitermes acajutlae* (Holmgren) y *N. nigriceps* (Haldeman), con referencia especial a inclusiones de cartón o nódulos encontrados dentro de la matriz de la galería de algunos nidos. El análisis de nutrientes de los nódulos muestra que estos tienen concentraciones altas de celulosa y bajas de cutina, en comparación con el cartón normal de los nidos. Los datos sostienen la hipótesis de que las inclusiones de los nódulos sirven como una forma facultativa de almacenamiento de alimento en algunos nidos de termitas de esas especies. Estos casos parecen representar una rara situación en la cual el alimento no es almacenado en pilas o cultivado por las termitas, sino masticado y parcialmente procesado e incorporado a la matriz del nido para consumo futuro.

The tropicopolitan termite genus *Nasutitermes* (Termitidae; Nasutitermitinae) is the most speciose of all isopteran genera, containing approximately 75 described species from the Neotropics alone (Araujo 1977). Unlike most termites, many species of *Nasutitermes* build arboreal carton nests composed of wood and salivary and fecal fluids (Light 1933), and occasionally other materials such as sand (Thorne & Haverty, pers. obs.). Most other nest-building termites build mounds on the ground (e.g., Emerson 1938), but nesting in trees has enabled species of *Nasutitermes* and several other genera to colonize and exploit a new habitat.

*Nasutitermes nigriceps* (Haldeman) is a geographically widespread termite, ranging at least from Panama north throughout the lowland forests of Central America into Mexico. It is also found on Jamaica and on Grand Cayman Island (Araujo 1977, Thorne et al. 1994). *N. acajutlae* (Holmgren), which is morphologically very similar to *N. nigriceps*, is found on Puerto Rico, the US and British Virgin Islands (BVI), Trinidad, and Guyana (Emerson 1925, Araujo 1977, Thorne et al. 1994). There are isolated reports of members of the *N. nigriceps* "complex" from other parts of South America, but a comprehensive taxonomic analysis of specimens is needed to verify species identity of the South American fauna.

Despite the abundance of *Nasutitermes* arboreal nests, the chemical composition of the carton material has not been examined in detail in any species (but see Becker & Seifert 1962 for data on ash and lignin content). Knowledge of the composition of the nest is fundamental in determining origin of nesting materials, cost of construction, variation among colonies and species, and ability of the termites to allocate components of their diet for nest construction.

A distinctive feature of some *N. acajutlae* and *N. nigriceps* nests is the presence of rounded carton inclusions or "nodules" within the typical gallery matrix (Hubbard 1877 pp. 268, 270, Andrews 1911 pp. 200-202, Emerson 1938 p. 264, Wolcott, cited in Martorell 1945 p. 361). These nodules appear to be of a similar carton construction as the rest of the nest, but they are a lighter brown color, are formed in dense concentric sheaths (Fig. 1), and they may possibly serve as a form of food storage (Hubbard 1877; Andrews 1911). Kemner (1929) interprets the presence of carton nodules in the Javan termite *Microcerotermes depokensis* Kemner as food storage structures. Noirot (1959) reported compact masses of wood fragments in the central cavity of nests of *Globitermes sulphureus* (Haviland). Some termite genera do store food as dried vegetative elements in specialized portions of their nests ("attics") [e.g., Hodotermitinae (*Hodotermes*, *Microhodotermes*, *Anacanthotermes*); Rhinotermitidae (*Psammotermes*); Termitidae: Amitermitinae (certain *Amitermes* and *Drepanotermes*), Nasutitermitinae (certain species of *Tumulitermes*, *Nasutitermes* and *Trinervitermes*)] (Noirot 1970, Bouillon 1970). The "fungus growing" termites (certain Macrotermitinae) culture fungus within the nest as a supplemental food source. Interestingly, some fungus growing termites store vegetative materials within the nest before they are included in the fungus garden (*Pseudacanthotermes*, *Acanthotermes*, some *Macrotermes*) (Grasse & Noirot 1951). If the *Nasutitermes* nodules described in this paper are indeed food reserves, they are not simply stored food but rather elements which have already been masticated and partially processed by the termites, then positioned within the nest matrix for future consumption.

In this paper we describe the architecture of *N. acajutlae* and *N. nigriceps* nests from sites in Panama and the BVI. Observations of the nodule inclusions are reported. Nutrient analyses of two nests without nodules and comparative chemical analyses of nodule material versus the surrounding "normal" carton matrix of two nests with nodules are presented and reported.

## MATERIALS AND METHODS

Eight *N. nigriceps* nests were collected within 5 km of the Panama Canal in 1980 and 1981; only one of these contained the distinctive nodules within the carton next matrix. This arboreal nest was collected from the Gigante East Peninsula near Barro

Colorado Island on 7 April 1981. The entire nest was pried from the host tree, placed within a plastic bag, and taken to the laboratory of the Smithsonian Tropical Research Institute on Barro Colorado Island. The nest was dissected by sequential shaving after being refrigerated for 24 hours to inactivate the termites (technique described in Thorne 1984).

Nest carton from four colonies (one *N. nigriceps* nest collected near Barro Colorado Island, Panama in 1981; three *N. acajutlae* nests collected in 1988 and 1989 on Guana Island, BVI) was analyzed in 1989-1990. Two of the nests (the *N. nigriceps* nest from Panama and a 1988 *N. acajutlae* nest from the BVI) contained nodules. Chemical composition of both the nodules and a sample of the more typical dark carton material was determined from those two nests, and samples of typical carton matrix from parts of two additional Guana Island *N. acajutlae* nests (which did not contain nodules) were also analyzed. Type of nest material examined is presented in Table 1.

### Materials and Methods for Nutritional Analyses of Nest Samples

In the laboratory, samples were dried at 60°C to constant mass (approximately 24 h). Dried samples were ground to pass through a 1 mm screen in a Wiley mill. A portion of each sample was dried at 105°C to determine percent dry matter and then placed in a muffle furnace for 3 h at 500°C to determine percent organic matter and ash (an estimate of total mineral content). In vitro organic matter digestibility, or percent fermentable substrate, was determined by the Tilley & Terry (1963) method as modified by Moore & Mott (1974). This analysis consists of a 48 h incubation under $CO_2$ at 39°C with an inoculant of steer rumen fluid followed by a 48 h acid-pepsin treatment to remove undigested microbes. The percent of organic matter that disappears during the 96 h is the in vitro organic matter digestibility.

Percentage of neutral detergent fiber (NDF: cellulose, hemicellulose, lignin and cutin) was measured by the Van Soest technique (Goering & Van Soest 1970) with decalin and sodium sulfite omitted (Golding et al. 1985). Analyses for percentages of acid detergent fiber (ADF: cellulose, lignin and cutin), potassium permanganate lignin, and cutin followed Goering & Van Soest (1970). Percent hemicellulose is estimated by subtracting ADF from NDF. Lipids were extracted with ethyl ether in a Goldfisch apparatus for 8 h. Percent concentrations of total (Kjeldahl) nitrogen and phosphorus were measured with a block digester (Gallaher *et al.* 1975) and an automated Technicon analyzer (Hambleton 1977). Energy content of food and feces was determined in a bomb calorimeter following standard procedure (Parr Instrument Co. 1960).

One sample was analyzed from each source of nest material. In each analysis, two subsamples were evaluated. Values for replicates of each sample were accepted within 1% relative error. Relative error is calculated as (a-b)/(a+b) where a and b are replicate values. Rarely, the values obtained for the duplicates were not within 1 relative percentage, in which case a third subsample was analyzed. Table 1 reports the mean of the analyzed values for each sample.

## RESULTS

### Nest Architecture

Nests built by *N. acajutlae* and *N. nigriceps* can be among the largest of any arboreal nesting *Nasutitermes*. Maximum dimensions of an ellipsoidal nest can approach 2 m in height and 1 m in girth (Thorne et al. 1994). The exterior of these nests is typically medium to greyish brown in color and irregularly mottled, generally with rather shallow bumps, unlike the dark nests with small bumps characteristic of the exterior of *N. corniger* (Motschulsky) and *N. costalis* (Holmgren) nests or the lighter brown, smooth shell typical of *N. ephratae* (Holmgren) (Thorne 1980; Haverty et al. 1990). Young nests may be difficult to identify to species, but differences in exterior appearance make it possible to visually discriminate most mature nests of *N. acajutlae* and *N. nigriceps* from those of *N. corniger*, *N. costalis*, or *N. ephratae*. The outer carton shell of nests of all of these *Nasutitermes* species has small pinpoint holes, visible if a piece is held up to a light. These holes presumably function in gas exchange.

The intercalated matrix of galleries within mature nests of *N. acajutlae* and *N. nigriceps* tends to be larger (chamber diam up to 2.1 cm) and with thicker carton walls (up to 0.6 cm near the exterior of a nest; exceeding 1.7 cm near the interior of the nest) than in nests of arboreal *Nasutitermes* found sympatrically with one or both of these species (*N. columbicus*, *N. corniger*, *N. costalis*, *N. ephratae*). The royal "cell" within the nest is often positioned near the central longitudinal axis of the nest, and frequently located in or near a branch fork or knothole of the host tree. In small to medium sized nests (< 60 cm diam) the royal cell is a distinctly thicker sphere or ellipsoid of layered carton (generally up to 12-15 cm in diam) surrounding the royal chamber. In nests exceeding 1 m on an axis the royal chamber can be embedded in the dense carton center of the nest, with the royal cell becoming indistinct from the remainder of the central, reinforced portion of the nest. We have not found distinguishing characters to differentiate nest architecture of *N. acajutlae* from *N. nigriceps*.

The carton-covered foraging trails built by large *N. acajutlae* and *N. nigriceps* colonies are wider and less regular than in *N. corniger*, *N. costalis*, or *N. ephratae*. Termites occupying small to medium sized *N. acajutlae* and *N. nigriceps* nests frequently build simple, linear trails 0.9-1.5 cm wide, thus they are indistinct from trails of *N. corniger*, *N. costalis*, or *N. ephratae*. However, trails leaving large nests of *N. acajutlae* and *N. nigriceps* are often broad (up to 14 cm in width) and deep (up to 8 cm from the tree to ceiling of the gallery). Trails from large nests are often highly irregular along the edges. Occasionally a "floor" is built as well so that the trail becomes a tube that can, for a limited distance, be separate from the tree or branch. As is typical for many arboreal *Nasutitermes*, tunnels built on the exterior of tree branches are frequently on the underside of the branch. We hypothesize that this minimizes disturbance by hard rainfall or by creatures traveling along the tops of branches. Building galleries in the "shade" of branches would also minimize desiccation from direct sunlight. A further advantage would be that foraging tunnels built on the undersides of branches would receive maximum moisture from rain running off the branch. This would be beneficial for *N. acajutlae* or *N. nigriceps* since they often live in relatively dry habitats (Thorne et al. 1994).

### Description of Nodules and Nest Population

We describe nodule inclusions in three nests: one *N. nigriceps* nest dissected in April, 1981 in Panama, one *N. acajutlae* nest dissected in July, 1988 on Guana Island, BVI, and a nest dissected on the island of Tortola, BVI in October, 1994 (nodules from the latter nest were not analyzed for nutritional content).

Photographs of the interior of the *N. nigriceps* nest collected in Panama are shown in Fig. 1. The nest was generally spherical, about 46 cm in diam, which placed it in a medium size category for conspecific nests in that area. Twenty nodule formations, 14 of which measured 3.0-4.8 cm in diam, but some as small as 1 cm diam, were removed from the nest. All nodules were positioned within 4-10 cm of the nest exterior. The nodules were of a uniform light brown color in contrast to the dark brown surrounding

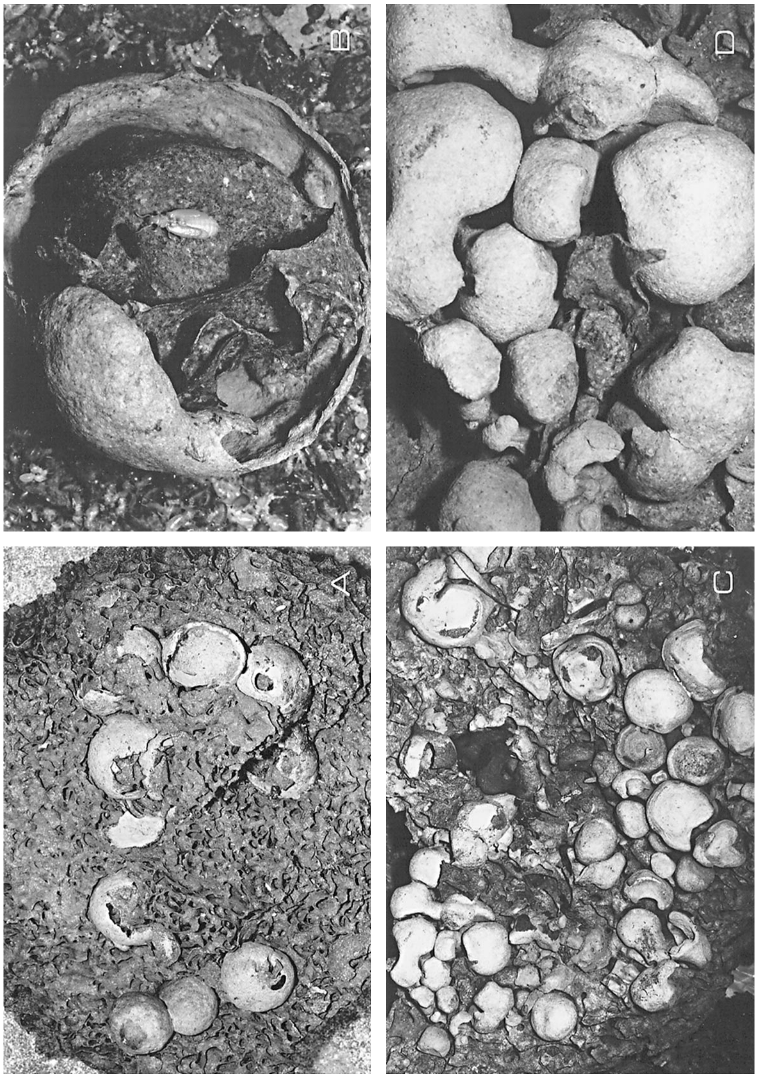

Figure 1. Photographs of nodules embedded within normal nest carton matrix in the *Nasutitermes nigriceps* nest collected in Panama in April 1981 (A,B) and in an *N. acajutlae* nest collected on Tortola, BVI in October 1994 (C,D).

nest matrix. Nodule shape was generally spherical although some had distortions or were irregular ellipses. The nest contained an active population of soldiers and workers, as well as a conspicuous brood of wingbud nymphs in the penultimate and ultimate instars. Many of the nymphs occupied the interiors of the nodule spheres. No reproductives, eggs or immatures were found within the nest.

The *N. acajutlae* nest on Guana Island was irregularly ellipsoidal, measuring approximately 1 m in height with a maximum diam of 75 cm. The nest contained a primary queen, developing nymphs of a variety of instars, many eggs and white larvae, and a large population of workers and soldiers. No primary king was retrieved but that is typical during field dissections because mature kings are small enough to retreat quickly and evade capture. The light-colored nodules were located in a zone surrounding the hard, inner core of the nest, all positioned at least 2 cm from the exterior nest wall. Many of the nodules were scalloped, possibly indicating consumption by termites. As with the *N. nigriceps* nest, immature termites occupied the interior of hollowed-out nodules.

An *N. acajutlae* nest collected on the island of Tortola, BVI was brought to us in several pieces during a field trip in October 1994. This large nest, estimated to have been just over a meter in height and about 80 cm in diam, contained eggs, white immature, soldiers, and workers. There were relatively few brachypterous nymphs, but numerous mature alates were present. The primary queen and king were not recovered, but the presence of egg caches suggests that the reproductives were present in the intact nest or in the portion of the host tree surrounded by the nest. This nest had clusters of nodules positioned within the inner perimeter of the nest (Fig.1 C, D) Again, the outer 2 cm or more of nest material was dark, more typical carton matrix with no nodules. Because the nest arrived in pieces, it was impossible to tell whether nodules were built in the center core of the nest.

We did not do nutrient analyses of nodule material from the Tortola nest, but we measured each of the 75 nodules that were retrieved. The distribution of nodule sizes recovered from this nest is shown in Fig. 2. Some of the irregularly spherical nodules in this nest were solid, dense material; most were hollowed to some extent as seen in the Panama and Guana Island nests. Hollowed nodules contained large numbers of immatures. Eight of the nodules from this nest were bilobed, as if two units had been constructed or fused together.

The nodules from all three of these nests were generally similar in size, shape, color, and position within the nest matrix. In each case immatures occupied excavated nodules.

## Chemical Analyses of Nest and Nodule Material

The most striking aspect of the nutrient composition of nest materials (Table 1) is the consistency among these nests. The only apparent differences are the higher cellulose and lower cutin concentrations in nodule samples than in carton samples and the higher in vitro organic matter digestibility values of the samples from Panama. No statistical analyses were performed because only two samples were available in each category. Hemicellulose was absent or present in only trace amounts in the samples, so was not included in Table 1. Nutrient composition of the nest material apparently does not change with age. The composition of recently constructed normal carton was very similar to that of old carton material from the North Bay and White Bay Beach nests on Guana Island. The high organic matter content indicates that little, if any, soil or sand is incorporated into these samples of nest or nodule material.

TABLE 1. NUTRIENT COMPOSITION OF NODULE AND NORMAL NEST CARTON SAMPLES[1]

| | Organic Matter | Cellulose | Lignin | Cutin | Lipids | Nitrogen | Phosphorus | In Vitro Organic Matter Digestibility | Energy |
|---|---|---|---|---|---|---|---|---|---|
| Panama-1981 | | | | | | | | | |
| Nodule | 96.0 | 30.9 | 35.8 | 5.1 | 1.6 | 0.66 | 0.06 | 15.0 | 19.6 |
| Normal nest carton | 94.5 | 16.6 | 31.9 | 30.9 | 0.8 | 0.73 | 0.06 | 10.2 | 20.7 |
| BVI-1988 | | | | | | | | | |
| Nodule | 95.2 | 29.9 | 37.5 | 9.0 | 0.8 | 0.75 | 0.04 | 5.6 | 19.8 |
| Normal nest carton | 94.5 | 16.9 | 40.9 | 17.7 | 0.8 | 1.03 | 0.08 | 6.2 | 20.7 |
| BVI-1989 North Bay Beach | | | | | | | | | |
| Interior, dense carton | 93.4 | 14.6 | 36.3 | 34.4 | 0.9 | 0.96 | 0.09 | 4.0 | 20.5 |
| Exterior, thin carton | 92.9 | 18.1 | 32.2 | 34.8 | 1.0 | 1.01 | 0.07 | 3.1 | 20.2 |
| BVI-1989 White Bay Beach | | | | | | | | | |
| New, thin carton | 91.1 | 18.7 | 36.5 | 27.4 | 1.2 | 0.70 | 0.05 | 4.2 | 19.5 |
| Fresh, very thin carton | 91.7 | 19.7 | 35.2 | 30.8 | 1.0 | 0.67 | 0.05 | 3.0 | 19.5 |
| Dry nest carton | 88.3 | 15.3 | 35.1 | 30.6 | 1.4 | 0.80 | 0.08 | 2.5 | 19.6 |

[1] All values are based on one sample, each analyzed in duplicate. If the values obtained for the duplicates were not within 1 relative percentage, a third replicate was analyzed. Means of the two or, rarely, three values are listed. All values are presented as percent dry matter except in vitro organic matter digestibility is expressed as percent organic matter and energy is expressed a kJ/g dry matter. Panama samples are from an *Nasutitermes nigriceps* colony; BVI (British Virgin Island) samples are from *N. acajutlae* colonies.

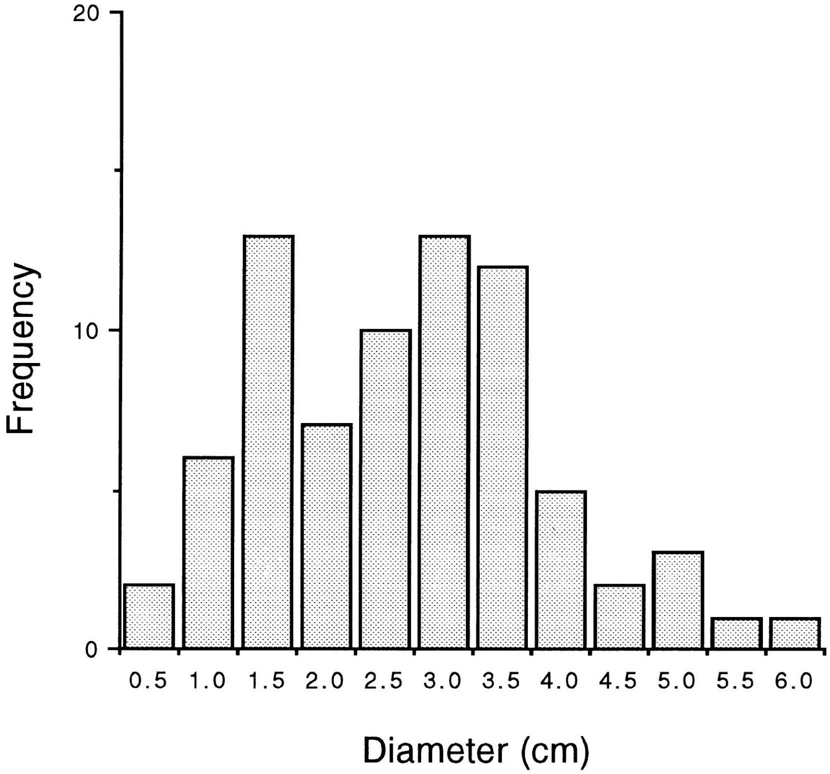

Figure 2. Size frequency distribution of nodules removed from the *Nasutitermes acajutlae* nest collected on the island of Tortola, BVI in October 1994 (N = 75; x = 2.6 ± 1.2 cm).

## DISCUSSION

*Nasutitermes acajutlae* and *N. nigriceps* are exceptional among termites in building distinctive inclusions or nodules within the normal carton matrix of their nests. The only other termite reported to build similar structures is the Javan termite *Microcerotermes depokensis* (Kemner 1929).

Two contrasts between the composition of nodules versus normal nest carton analyzed in this study may be biologically significant. First, the nodule samples have lower cutin and higher cellulose percentages than do samples of the surrounding, dark carton matrix. Cutin degradation is not possible for most organisms except some specialized fungi; digestion of cutin by termites is unknown (Breznak, pers. comm.). The differences in cutin and cellulose percentage may indicate that the termites are constructing the nodules from materials with greater digestibility. The relatively high cutin percentages in typical carton probably enhances water-proofing and construction strength. It is unlikely that the difference in cutin abundance is due to transfer of waxes from the insect exocuticle to the nest walls. The percentage of cutin in fresh, newly constructed carton (having minimal opportunity for contact transfer of waxes from passing insects) does not differ markedly from that of old, dense, interior carton (see samples from North Bay and White Bay Beach nests, Guana Island, BVI in Table 1).

A second distinction is that both the nodule sample and the normal gallery within the nodule sample from Panama have higher in vitro digestibility than do any of the BVI samples. This may reflect species differences in carton processing, or a difference in diet among the two populations (*N. acajutlae* sampled from Guana Island were feeding substantially on sea grape, *Coccoloba uvifera*, the diet of the *N. nigriceps* from Panama is unknown). Clearly, further sampling and geographic variation within each species must be examined before differences of this type can be further evaluated.

Hubbard (1877) and Andrews (1911) hypothesized that these *Nasutitermes* nodules serve as food storage. Kemner (1929) came to a similar conclusion in the case of *Microcerotermes depokensis*. The food storage hypothesis is supported by the higher cellulose content of nodules in comparison to surrounding nest carton in both *N. acajutlae* and *N. nigriceps*. It is difficult to know the conditions under which the nodules might be naturally consumed in a nest, but 0.3 g portions of both *N. acajutlae* and *N. nigriceps* nodules offered to 100 workers of *N. acajutlae*, *N. nigriceps*, *N. costalis*, and *Zootermopsis nevadensis* (Hagen) were consumed in the laboratory within 24 h, and consumed by 100 *Reticulitermes flavipes* (Kollar) workers within 48 hr (N=3 per species). These species did not consume the normal carton of either *N. acajutlae* or *N. nigriceps* nests.

Termite nest material can be used as nutritional food reserves in some species. Hegh (1922) commented that termites in mature colonies of *Microcerotermes fuscotibialis* (Sjostedt) eat the internal walls of their nests during times of food stress. Noirot (1970) reported that central walls of *Cephalotermes rectangularis* (Sjostedt) nests can be used to culture the termites in the laboratory.

The function of nodules and circumstances under which they are constructed are difficult to identify because they are found so rarely. In both Panama and the BVI, examination of nests of approximately the same size, in the same local area, at the same season never revealed another live colony with nodules. Because young were found within the nodules of both *N. acajutlae* (white immatures instars 1-3) and *N. nigriceps* (developing alate nymphs) the nodule food reserves may be sequestered for juveniles. Comparable nests with immatures, however, did not have nodules. Nodule construction may be influenced by individual colony health, age, microhabitat, food resources, caste proportions, or population size. Even among colonies producing nodules, they may be ephemeral within a nest. Nodules may only be present seasonally, stockpiled as food reserves and then consumed during times of high demand (as when alate brood is present), when food is scarce, or when travel from the nest is physiologically expensive (as in a drought). It is notable that the only two *Nasutitermes* species known to construct these nest inclusions are the closely related species *N. acajutlae* and *N. nigriceps*, both of which can occupy dry and thus potentially stressful environments (Thorne *et al.* 1994). The facultative ability to store food in nodules, combined with an exceptional desiccation tolerance of individuals, may contribute to the survival of these two *Nasutitermes* species in arid or otherwise marginal habitats not colonized by other members of the genus.

## ACKNOWLEDGMENTS

We extend sincere thanks to Dr. and Mrs. Henry Jarecki and the staff of The Guana Island Club for their support and hospitality during the course of this project. John A. Breznak, Michael I. Haverty, and James D. Lazell provided constructive input and productive discussions. Field assistance was contributed by James Egelhoff, Thomas Jarecki, and Ralph Rusher. Portions of this research were funded by The Conservation Agency through a grant from the Falconwood Foundation, The Smithsonian Tropical Research Institute, NSF grant DEB-8607407 to BLT, and by a cooperative agreement between the University of Maryland and the Pacific Southwest Research Station, U.S. Department of Agriculture.

## REFERENCES CITED

ANDREWS, E. A. 1911. Observations on termites in Jamaica. J. Anim. Behav. 1: 193-228.

ARAUJO, R. L. 1977. *Catalogo dos Isoptera do Novo Mundo*. Academia Brasileira de Ciencias, Rio de Janeiro, 92 pp.

BECKER, V. G., AND K. SEIFERT. 1962. Ueber die chemische zusammensetzung des nest - und galeriematerials von termiten. Ins. Soc. 9: 273-289.

BOUILLON, A. 1970. Termites of the Ethiopian Region, pp. 73-125 *in* K. Krishna and F. M. Weesner [eds.] *Biology of Termites, Volume II*. Academic Press, N.Y.

EMERSON, A. E. 1925. The termites of Kartabo, Bartica District, British Guiana. Zoologica 6: 291-459.

EMERSON, A. E. 1938. Termite nests. A study of the phylogeny of behavior. Ecol. Monogr. 8: 247-284.

GALLAHER, R. N., C. O. WELDON, AND J. G. FUTRAL. 1975. An aluminum block digester for plant and soil analysis. Soil Sci. Soc. American Proc. 39: 803-806.

GOERING, H. K., AND P. G. VAN SOEST. 1970. Forage fiber analyses (Apparatus, reagents, procedures, and some applications). Agric. Handbook 379. U.S.D.A., Washington, D.C.

GOLDING, E. J., M. F. CARTER, AND J. E. MOORE. 1985. Modification of the neutral detergent fiber procedure for hays. J. Dairy Sci. 68: 2732-2736.

GRASSE, P. P., AND C. NOIROT. 1951. Nouvelles recherches sur la biologie divers Termites champignonnistes (Macrotermitinae). Ann. Sci. Nat. Zool. Biol. Animale [11] 13: 291-342.

HAMBLETON, L. G. 1977. Semiautomated method for simultaneous determination of phosphorus, calcium and crude protein in animal feeds. J. Assoc. Off. Agric. Chem. 60: 845-852.

HAVERTY, M. I., B. L. THORNE, AND M. PAGE. 1990. Surface hydrocarbon components of two species of *Nasutitermes* from Trinidad. J. Chem. Ecol. 16: 2442-2450.

HEGH, E. 1922. *Les Termites*. Imprimerie Industrielle & Financiere, Bruxelles.

HUBBARD, H. G. 1877. Notes on the tree nests of termites in Jamaica. Proc. Boston Soc. Nat. Hist. 19: 267-274.

KEMNER, N. A. 1929. Ans der Biologie der Termiten Java. 10th Congr. Int. Zool., Budapest, 2: 1097-1117.

LIGHT, S. F. 1933. Termites of Western Mexico. Univ. of California Publ. in Entomol. 6: 79-164.

MARTORELL, L. F. 1945. A survey of the forest insects of Puerto Rico. Part II. The Journal of Agriculture of the University of Puerto Rico. The Agricultural Experiment Station, Rio Piedras, P.R. 29: 355-608.

MOORE, J. E., AND G. O. MOTT. 1974. Recovery of residual organic matter from in vitro digestion of forages. J. Dairy Sci. 57: 1258-1259.

NOIROT, C. 1959. Le nid de *Globitermes sulphureus* Haviland au Cambodge. Ins. Soc. 6: 259-269.

NOIROT, C. 1970. The nests of termites, pp. 73-125 *in* K. Krishna and F. M. Weesner [eds.] *The Biology of Termites, Volume II*. Academic Press, N.Y.

PARR INSTRUMENT CO. 1960. Oxygen bomb calorimetry and combustion methods. Technical Manual Parr Instrument Company 130: 1-56.

THORNE, B. L. 1980. Differences in nest architecture between the Neotropical arboreal termites *Nasutitermes corniger* and *Nasutitermes ephratae* (Isoptera: Termitidae). Psyche 87: 235-243.

THORNE, B. L. 1984. Polygyny in the Neotropical termite *Nasutitermes corniger*: life history consequences of queen mutualism. Behav. Ecol. Sociobiol. 14: 117-136.

THORNE, B. L., M. I. HAVERTY, AND M. S. COLLINS. 1994. Taxonomy and biogeography of *Nasutitermes acajutlae* and *N. nigriceps* (Isoptera: Termitidae) in the Caribbean and Central America. Ann. Entomol. Soc. America 87: 762-770.

TILLEY, J. M. A., AND R. A. TERRY. 1963. A two-stage technique for the *in vitro* digestion of forage crops. J. British Grassl. Soc. 18: 104-111.

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