DIFFERENCES IN NEST ARCHITECTURE BETWEEN THE NEOTROPICAL ARBOREAL TERMITES *NASUTITERMES CORNIGER* AND *NASUTITERMES EPHRATAE* (ISOPTERA: TERMITIDAE)

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Introduction

Nests of the Neotropical termites *Nasutitermes corniger* (Motschulsky) and *N. ephratae* (Holmgren) have distinctive external and internal architectures. The differences are useful field characters because they are apparent in all but the smallest (<15 cm diameter) nests.

N. corniger and *N. ephratae* are sympatric throughout much of their range. *N. corniger* has been reported from México (Snyder 1949), Guatemala (Becker 1953), Honduras (Snyder 1949), Costa Rica (Holmgren 1910, Snyder 1925), Panamá (Motschulsky 1855, Banks 1918), Venezuela (Snyder 1959), and Bolivia (Snyder 1926). *N. ephratae* reportedly ranges from México (Becker 1961) to Brazil (Mathews 1977), with collections from Honduras (Snyder 1949), Costa Rica (Snyder 1925), Panamá (Banks 1918), Venezuela (Snyder 1959), Trinidad (Snyder 1949), Guyana (Banks 1918, Emerson 1925), Surinam (Holmgren 1910, Emerson 1925), and Bolivia (Snyder 1926).

Both *N. corniger* and *N. ephratae* build arboreal carton nests in lowland habitats.[1] The general structure of arboreal *Nasutitermes* nests has been described by Emerson (1938) and Noirot (1970). The bumpy exterior carton of *N. corniger* nests was distinctive to early isopterists working in Panamá (Dudley & Beaumont 1889a,b; Dietz & Snyder 1923; Snyder & Zetek 1924). *N. ephratae* nests were described briefly by Becker (1953) and by Mathews (1977).

Dietz and Snyder (1923) apparently found *N. ephratae* colonies in

[1] *N. ephratae* is also capable of building mounds (pers. obs. from a savannah near Barinas, Venezuela).

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the field only rarely, but they conclude, "In texture and general internal structure the nests and runways of *N. ephratae* are inseparable from those of *N. corniger*". Based on a larger sample size, this paper presents evidence that colonies of the two species can be distinguished solely on the basis of nest architecture.

This study is based on work done in Costa Rica and the Republic of Panamá. Entire *Nasutitermes* nests of a variety of sizes were collected, measured, weighed, and completely dissected. Data presented in this paper are based on 102 *N. corniger* colonies and 29 *N. ephratae* colonies collected in second-growth areas near Barro Colorado Island, Panamá. Less quantitative but corroborating observations were made at La Selva, Sirena, and Llorona, Costa Rica and in a variety of places in central Panamá.

Both species of termite were identified by Dr. Kumar Krishna at the American Museum of Natural History, N.Y. In addition, specimens of *N. corniger* compare favorably with the syntype specimens (Museum of Comparative Zoology, Harvard University). Morphological differences between the two species are distinct among alates or reproductives, but subtle when comparing soldiers. *N. corniger* alates have black wings, dark bodies, and ocelli which are located relatively far from the eyes (by a distance of about twice the diameter of an ocellus) (Banks 1918, Dietz & Snyder 1923, Snyder 1959). *N. ephratae* alates have yellow-brown wings, brown bodies, and ocelli located close to the eyes (Banks 1918, Emerson 1925, Snyder 1959, Mathews 1977). Soldiers are differentiated on the basis of head shape (Banks 1918) or amount of tergal pubescence (Snyder 1959), but these differences are not always prominent. In alcohol, *N. ephratae* soldier heads turn reddish-brown while heads of *N. corniger* soldiers remain a rich, dark brown (pers. obs.). Voucher specimens from this study have been deposited at the Museum of Comparative Zoology (*N. corniger* nest numbers 3, 4, 23, 46, 80; *N. ephratae* nest numbers 22, 28, 31, 92).

Differences in External and Internal Architecture

The dark brown surface of an *N. corniger* nest is coarse with small bumps covering the entire exterior [Figure 1a]. Nests tend to be roughly spherical when small (diameter $\leqslant$20 cm), and grow more ellipsoidal as they enlarge. (The largest *N. corniger* nest dissected in this study was $68 \times 46 \times 34$ cm^3; 28.0 kilos.) Localized additions to

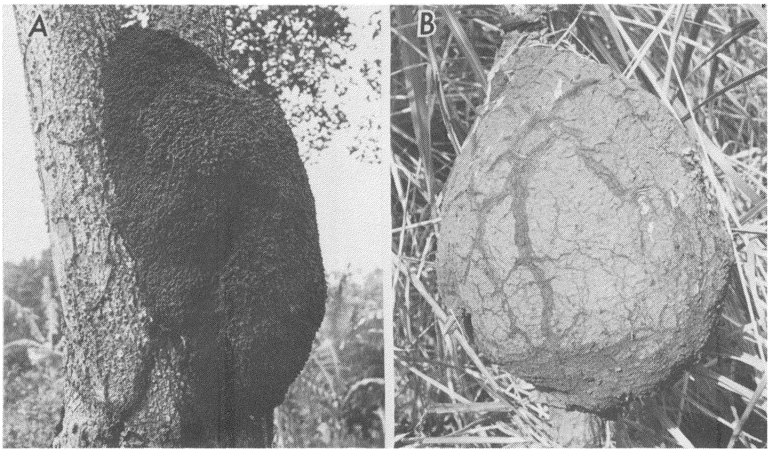

Figure 1. A. *N. corniger* nest; B. *N. ephratae* nest. Note the differences in surface texture and contour.

the nest may generate lobes on the contour of the surface.

N. ephratae nest exteriors are a lighter brown and distinctly smoother than *N. corniger* surfaces [Figure 1b]. The form of *N. ephratae* surface carton creates a leathery appearance. Nests of *N. ephratae* are more evenly spherical or ellipsoidal than *N. corniger* nests. The smooth, rotund silhouette is reformed by the termites if a portion of the nest is damaged or enlarged.

Internally, *N. corniger* nests are heavily reinforced (with thick, dense carton) around the queen cell [Figure 2a]. The queen's chamber measures from 1.5 to 8.0 cm at its maximum width, and from 0.6 to 0.9 cm in height. The queen cell is usually located in a central portion of the nest, often near (and sometimes within) the tree trunk or branch which hosts the nest. Hard, thick carton surrounds the queen cell and can continue out radially from the chamber for 2–20 cm, depending on nest size and age. Carton density decreases somewhat with distance from the queen cell, although this pattern is variable. In small, young nests the dense queen cell wall is only 1–2 cm thick. There is a rapid transition from thick queen cell carton to thin surrounding carton in such nests.

Outer portions of an *N. corniger* nest can be relatively thin, although the termites may reinforce areas with thicker material if the nest is damaged by a predator. Older nests tend to be harder

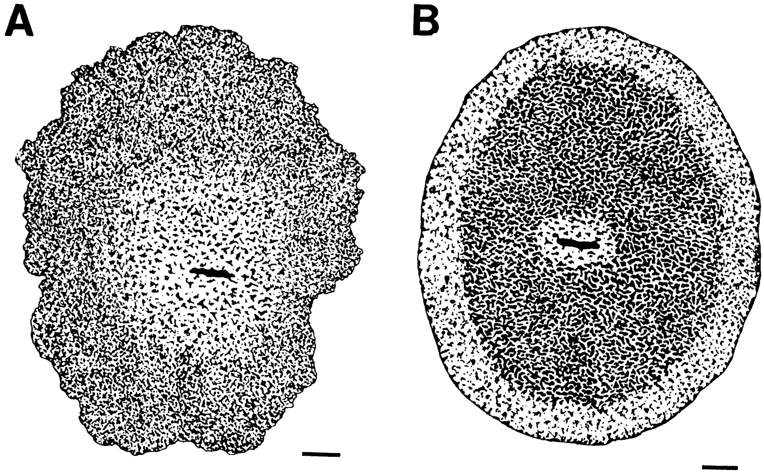

Figure 2. Diagrams of a cross section through the interior of a typical A. *N. corniger* nest; B. *N. ephratae* nest. Scale = 4 cm. Black indicates open galleries, white represents carton. The queen chamber and surrounding cell is located near the center of each colony. Differences in architecture and carton density are described in the text.

than younger nests (also observed by Beaumont (Dudley & Beaumont 1889a)). The nest galleries are relatively small (usually ⩽0.7 cm in height) throughout each colony, although they sometimes increase in size near the outer edge of a nest. The layer of bumpy surface carton is attached directly to each wall of the intersecting internal galleries. The entire interior of *N. corniger* nests is constructed of dark brown carton.

The queen cell of an *N. ephratae* colony is also located near the center of the nest [Figure 2b, 3], but the remainder of the internal architectural design diverges from the *N. corniger* pattern. An *N. ephratae* royal chamber is surrounded by a 1.0–1.6 cm capsule of hard, dense carton. This queen cell is suspended in a matrix of thin carton composed of relatively large galleries and chambers. The transition in carton density between the queen cell and surrounding thin gallery network is abrupt. The interior carton of *N. ephratae* nests is a lighter brown than that of *N. corniger*.

Except in very small *N. ephratae* nests (diameter <15 cm), the thin carton nest interior is encased in a 4.0–6.5 cm outer band of very hard, thick carton containing only small galleries (diameter

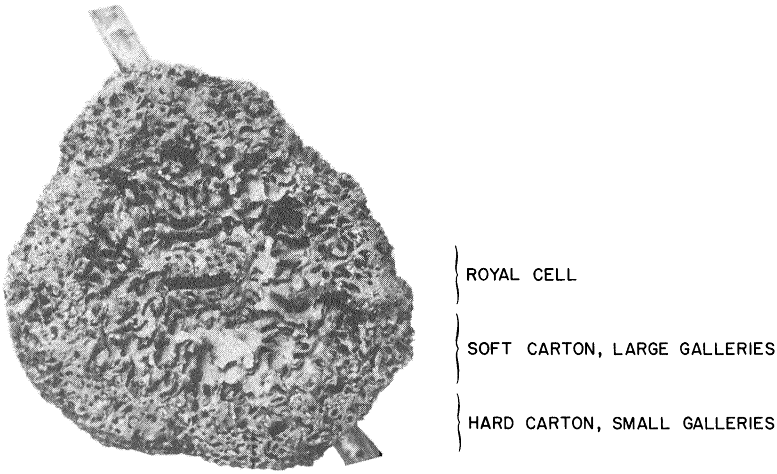

Figure 3. Photo of the interior of a small *N. ephratae* nest. The thin exterior envelope has been removed.

$\leqslant$0.5 cm). This tough layer protects the thin internal carton and is probably an excellent defensive barrier against vertebrate predators.

The smooth surface covering on the outside of an *N. ephratae* nest encases the dense layer of carton but unlike *N. corniger* nests, it is not attached to the internal carton at the terminus of each gallery. Rather, the surface layer is a "superficial envelope" (Noirot 1970). This envelope is easily removed in large sections. Inspection of a piece of the envelope reveals tiny perforations over the entire surface. (Beaumont (Dudley & Beaumont 1889a) noticed small 'apertures' in the exterior carton of *N. corniger* nests.) It is possible that these holes function in air exchange and thermoregulation within the colony.

The relationship between nest volume (estimated using the formula for an ellipsoid) and weight is different between *N. corniger* and *N. ephratae* (based on non-overlap of the 95% confidence limits on the slopes of the principal axes [See Figures 4 and 5] and an analysis of variance on the ratio of nest volume: weight indicating that differences between species are significant at $p < 0.01$). On average, *N. ephratae* invests less weight in carton per unit volume of nest.

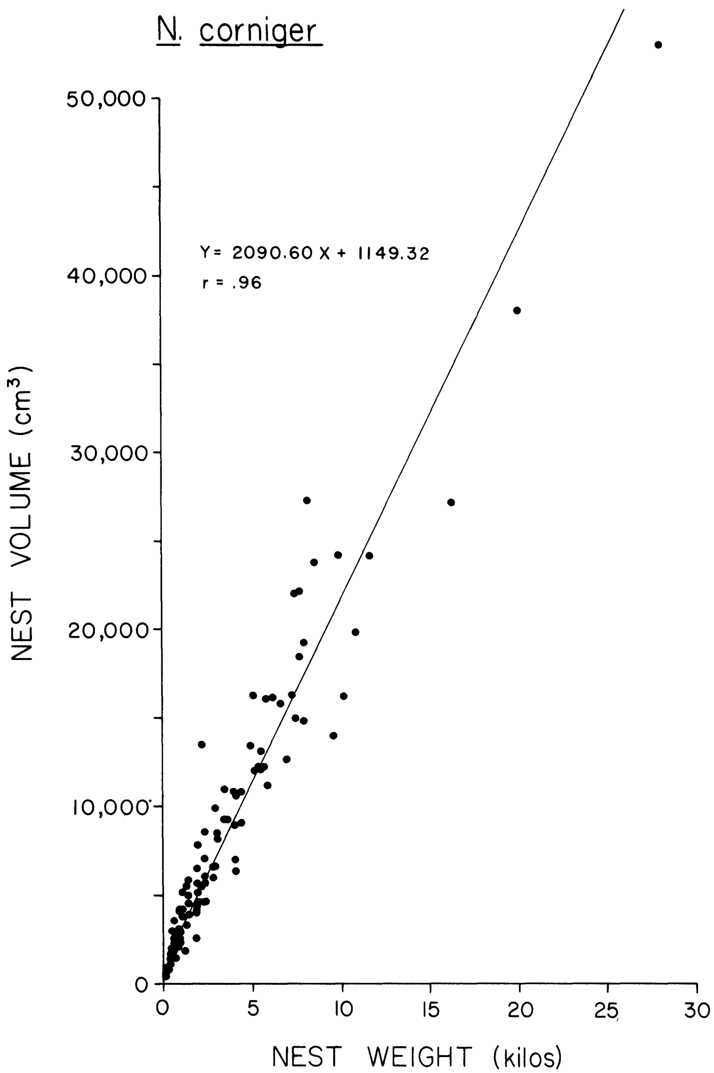

Figure 4. The relationship between nest weight and volume in *N. corniger*. The equation of the first principal axis (based on correlation analysis) is given. The correlation coefficient (r) is highly significant ($p < 0.001$). The 95% confidence limits on the slope of the principal axis are L_1 = 1976.84; L_2 = 2218.26.

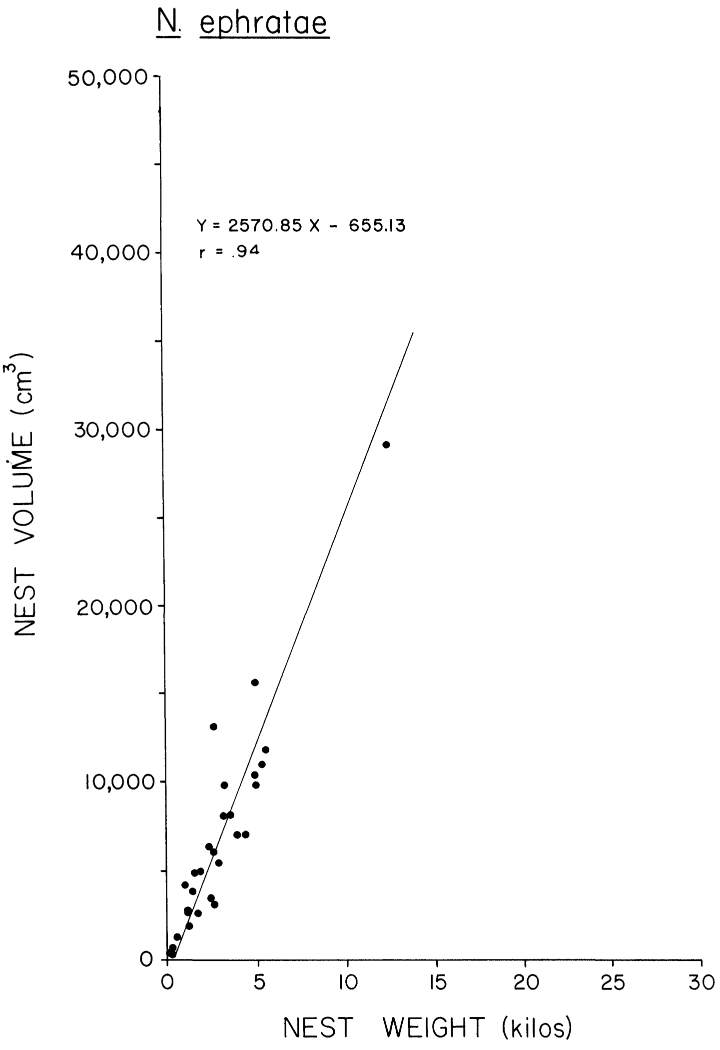

Figure 5. The relationship between nest weight and volume in *N. ephratae*. The equation of the first principal axis (based on correlation analysis) is given. The correlation coefficient (r) is highly significant ($p < 0.001$). The 95% confidence limits on the slope of the principal axis are $L_1 = 2268.83$; $L_2 = 2965.61$.

Conclusions

Arboreal nests of the sympatric Neotropical termites *N. corniger* and *N. ephratae* are structurally consistent within species but distinctly different between species. Except in very small nests, the exterior and interior differences are reliable, useful field characters for differentiating two species that can otherwise be difficult to distinguish without alates or primary reproductives. It would be interesting to examine the nest architecture of other arboreal *Nasutitermes* in the New World[2] for possible phylogenetic trends.

NOTE ADDED IN PROOF: Chemosystematic analysis of soldier head monoterpenes and diterpenes also reveals distinctive and reproducible differences between *N. corniger* and *N. ephratae* in most cases. However, several *N. corniger* nests have yielded soldiers with *corniger*-like monoterpenes and *ephratae*-like diterpenes (G. Prestwich, B. Thorne, and B. Bentley, unpublished).

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[2]The exterior surfaces of *N. nigriceps* and *N. columbicus* colonies in Panamá are distinct from *N. corniger* and *N. ephratae* nests (pers. obs.), but internal structure has not been investigated.

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