Comparative Nesting Habits and Colony Composition of Three Arboreal Termites (Isoptera: Termitidae) in Trinidad & Tobago, West Indies

by

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ABSTRACT

In a survey of arboreal termites in different habitats in Trinidad & Tobago, West Indies, three species predominated: *Microcerotermes arboreus*, *Nasutitermes corniger* and *N. ephratae*. *M. arboreus* accounted for most colonies in a pine plantation, while *N. corniger* predominated in farmland and mangrove. The two species had roughly equal proportions, overall, at several broadleaf-forest sites. A fourth species, either *Termes hispaniolae* or *T. fatalis*, appeared only in broadleaf forest.

Each of the three common species shows wide variance in nest height within habitats. The overall pattern is consistent with much greater within-species variation among habitats than among species in the same habitat. In no habitat is there a clear height differentiation among species.

Analysis of colonies shows the expected similarity in the two species of nasute-termites. Both showed a mean soldier fraction of 17% among adults, while in *M. arboreus* only 3% of adults were soldiers. Features of nest structure may be related to this difference.

INTRODUCTION

In this paper we seek to contribute to the understanding of Caribbean termites by examining habitat preferences, nest-height pattern and colony composition of three arboreal termites in Trinidad & Tobago.

There are four main categories of termite nest sites (Noirot 1970): within wood, underground, on the soil surface, and arboreal. The latter are found on tree trunks and branches between the soil surface and the canopy. Arboreal-nesting termites almost always connect the nest to the soil surface by covered

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galleries, through which workers and soldiers can move unexposed to and from foraging sites. Height above the ground would thus seem to be an important parameter in nest-site choice, yet it has been all but neglected in treatments of nesting habits.

A preliminary survey showed that three species account for almost all arboreal colonies in both islands: *Microcerotermes arboreus* Emerson (Termitidae: Termitinae), *Nasutitermes corniger* (Holmgren) (Termitidae: Nastutitermitinae) and *N. ephratae* (Holmgren). Aside from these, only *Termes hispaniolae* and/ or *T. fatalis* (Termitidae: Termitinae) showed any significant presence in any habitat, always nesting at or very close to ground level.

Microcerotermes and *Nasutitermes* are large, pantropical genera. *M. arboreus* Emerson (Termitinae), *N. corniger* (Holmgren) (Nastutitermitinae) and *N. ephratae* (Holmgren) are all known from Central America to Amazonia (in the case of *N. corniger* to northern Argentina) and the continental islands of Trinidad and Tobago (Constantino 2009). They are also recorded from the Antilles as follows: a) *M. arboreus* in Puerto Rico and Hispaniola, b) *N. corniger* throughout most of the Greater and Lesser Antilles, and c) *N. ephratae* from some of the Lesser Antilles (Scheffrahn *et al.* 1994).

Nesting and other ecological information on members of both genera are reviewed by Grassé (1984), and Lubin (1983) summarized the biology of *Nasutitermes*. Few data are available on the longevity of termite colonies, although some have been shown to persist for more than 20 years. Long-lived colonies are especially noted among the Nasutitermitinae, in which 40 years appears not be an uncommon age (Grassé 1984:149).

Although each studied species in these genera appears to have a characteristic predominant nesting habit, variation is also known within some species (Noirot 1970). Nest site appears to have little effect on the structure of *Microcerotermes* nests, which usually comprise a simple, homogeneous matrix around a specialized royal cell, with no distinct outer envelope (Noirot 1970, Grassé 1984). Arboreal nests of *Nasutitermes* usually comprise a fairly homogeneous matrix of thin-walled chambers around a harder, thicker-walled section that encloses a distinct royal cell, the whole surrounded by a very thin, brittle envelope.

The caste system of the three species is characteristic of the Termitidae (Noirot 1969, Grassé 1984). As a rule in social insects, the fraction of individuals outside the nest at any given time tends to be small. In termites, this is hard to corroborate, yet the fraction is believed to be fairly constant (Grassé 1984). This allows for a minimal margin of error in determining both caste structure and colony size.

MATERIALS AND METHODS

We surveyed arboreal termites at 11 sites of six habitat types:

1. Mixed closed-canopy broadleaf forest at elevations of about 100-500 m at five sites: a) the Maracas Valley and nearby Mt St Benedict in the Northern Range of Trinidad (10°40'N 61°24'W), b) Mount Harris in the Central Range of Trinidad (10°30'N 61°07'W), c) Bushbush, a peninsula within the Nariva Swamp along the east coast of Trinidad (10°23'N 61°02'W), d) between Charlotteville and Hermitage near the northeast end of Tobago (11°19'N 60°33'W), and e) between Roxborough and Parlatuvier near the high point of the Central Range of Tobago (11°17'N 60°36'W). Data from sites (d) and (e) are combined. Forest at the Mount Harris site appeared to be younger than at others. Bushbush has sandy soil and an abundance of cocorite palms (*Attalea maripa*), an indicator of well-drained, nutrient-poor soil (Aitken 1973; Henderson *et al.* 1995:162).

2. Dry forest close to sea level on the island of Little Tobago off the northeast end of Tobago (Boodram & Oatham, unpubl.) (site f, 11°18'N 60°31'W).

3. A mangrove forest east of Scarborough, Tobago (site g, 11°11'N 60°44'W).

4. A neglected rubber plantation of tall trees and little understorey in southwestern Trinidad (site h, 10°28'N 61°'37'W).

5. A pine (*Pinus caribbensis*) plantation at about 200-300 m on Mt St Benedict (site i, 10°41'N 61°24'W).

6. Mixed farmland below about 100 m at two sites: j) south of the Northern Range of Trinidad near site (a), and k) southwest of Scarborough, Tobago (10°10'N 60°47'W).

In order to have an indication of whether arboreal termites are comparably abundant in the two islands of Trinidad and Tobago, one of us (CKS) did a rough walking survey of living colonies in broadleaf forest in several bouts at sites (a), (d) and (e).

In a preliminary survey of the termites and their nests, we determined that a fresh-looking nest with an intact periphery almost always contained a colony, while defunct nests showed definite physical damage. In later recording data, we relied mainly on this rule to distinguish active from defunct nests, only occasionally testing directly for the presence of termites. The identifying characters of the species are found in Emerson (1925). However, most colonies of arboreal termites in Trinidad & Tobago are reliably identified on the basis of external nest features, so that we only occasionally collected samples of termites for closer examination. While *N. corniger* and *N. ephratae* nests are readily distinguished by the surface texture of the envelope (Thorne 1980), the sympatric *N. acajutlae* (Holmgren) makes a nest hardly distinguishable from that of *N. corniger* (Clarke 1991; pers. obs.). However, *N. acajutlae* is the much less common of the two in Trinidad (Clarke 1991) and presumably in Tobago, and was not encountered in our sampling. We are thus confident that few if any of our *N. corniger* are mis-attributed.

In a walking survey at each site, we recorded all apparently active colonies of each species.

A mature *N. corniger* colony often occupies several queenless auxiliary nests (=calies) in addition to the queen-containing main nest (Clarke 1990, Roisin & Pasteels 1986). Given the very large sizes that *N. ephratae* nests can reach and their tendency to spatial isolation, it seems less likely that this species commonly builds auxiliary nests. However, we note that *M. arboreus* nests of disparate sizes are often found close to each other, so that the use of auxiliary nests seems very probable. Although it was our intention to survey primary nests only, it was impractical to confirm each nest's status by rigorous dissection. In order to minimize the number of auxiliary nests included in our samples, where two or more conspecific nests occupied the same or adjacent trees we disregarded all but the largest. In addition, we disregarded any nests with a volume less than about two liters.

"Nest height" here refers to the minimum walking distance from the center of the nest to the ground or, in the case of mangrove, the high-tide level. In some cases this was greater than simple height above ground. We estimated nest height by mentally advancing up the tree in two-meter increments. As a control against any drifting bias in perception, one of us occasionally stood against the trunk for scale, while the other estimated height.

All collecting of live colonies was in February-March 1993 (early dry season). We removed nests as completely as possible, usually in large fragments.

Each nest was sealed in a plastic bag and frozen to kill the termites. After re-thawing the nest, we did a gross dissection in order to observe internal nest structure and search for the queen(s). Although we usually succeeded in finding the queen (never more than one per colony in this study), this was not a key part of the study, so that the effort was not rigorous.

After the initial dissection, we weighed the nest, crushed it manually to a gravel-like consistency, thoroughly mixed the fragments, and took a sample of about 25 g for caste-structural analysis. This latter procedure consisted of weighing the sample (to ±0.05 g) and then counting individuals of each adult caste: workers, soldiers and reproductives.

In Grassé's (1984:151; our translation) view, "The censusing of a colony fragment and then estimating the total by multiplication is a most regrettable method that involves great sources of error." We believe that homogenization of the nest and its contents overcomes this line of objection. Although the subset of absent foragers and those successfully fleeing the nest is unaccounted for, this almost certainly represents a relatively insignificant fraction of the total colony.

RESULTS

The preliminary survey of summed abundance in comparable broadleaf forest showed 81 colonies in 157 min of search in Trinidad and 86 colonies in 193 min of search in Tobago. This rough test is consistent with the hypothesis that the two islands do not differ in the density of arboreal termites.

Table 1 shows the relative abundance of the three species at each study site. We noted colonies of a fourth arboreal termite, *Termes hispaniolae* (Banks) or

Table 1. Relative abundance of colonies of three arboreal termites in different habitats of Trinidad & Tobago. Letters below habitat types indicate study sites named in the Materials and Methods.

	Mixed broadleaf forest				Dry forest	Mangrove	Rubber	Pine	Farmland	
	a	b	c	d+e	f	g	h	i	j	k
M. arboreus	152	80	113	22	32	0	5	177	23	10
N. corniger	105	16	111	54	68	52	36	1	116	55
N. ephratae	37	8	4	36	14	0	5	2	3	1
Total	294	104	228	112	114	52	46	180	142	66

Table 2. Mean ± SD (above) and modal (below) nesting heights of three arboreal termites in different habitats of Trinidad & Tobago. Cells for which we have fewer than 10 data are left blank. Letters below habitat types indicate study sites named in the Materials and Methods. Complete data-set available at http:\\www.ckstarr.net\cks\2010-TERMITES.xls .

	Mixed broadleaf forest				Dry forest	Mangrove	Rubber	Pine	Farmland	
	a	b	c	d+e	f	g	h	i	j	k
M. arboreus	3.60±2.90 2 (n=173)	4.65±2.22 3-4 (n=91)	2.75±1.66 2 (n=121)	1.45±2.16 1 (n=20)				2.09±1.34 1 (n=186)	3.04±1.94 2 (n=24)	2.27±2.41 2 (n=11)
N. corniger	4.13±2.12 5 (n=168)	5.81±4.46 none (n=16)	4.69±2.80 3 (n=132)	2.66±3.14 1 (n=70)	1.22±1.29 1 (n=63)	1.44±1.36 1 (n=52)	8.37±5.55 2-4 (n=87)		3.71±2.06 4 (n=175)	1.44±2.38 0 (n=66)
N. ephratae	3.87±3.06 2 (n=39)			1.60±1.89 2 (n=37)						

T. fatalis Linnaeus, in small numbers in broadleaf forest only.

Each species showed wide variance in nest height at each site (Table 2, Fig. 1).

The data allow for 10 pairwise comparisons between species in the same habitat. Just three of these (between *M. arboreus* and *N. corniger* at sites a, c and k) show a significant difference (Mann-Whitney test, $p \leq 0.05$), although the differences are not consistent.

Tables 3 and 4 show statistical comparisons among sites in *M. arboreus* and *N. corniger*, respectively. In *N. ephratae*, median height was greater at site (a) than sites (d+e). Of the 58 pairwise comparisons, 43 show a significant difference. Furthermore, in the seven pairs of sites showing a difference in two or three species, the differences are all consistent.

We found several active nests resting directly on the soil surface. In most cases, the presence of wood fragments embedded in the base indicated that the nest had originated on a tree trunk or branch that had since fallen (from an unknown height).

Table 3. Comparison of height distributions of *Microcerotermes arboreus* nests among sites in Trinidad & Tobago. Sites (a-e) are mixed broadleaf forest. Site (i) is a pine plantation. Sites (j-k) are farmland. Where two sites differ significantly in median height, the site with the greater median is indicated in the cell. Cells marked in bold are those for which there is also a significant difference in *Nasutitermes corniger* (Table 4).

	b	c	d+e	i	j	k
a	b		**a**	a		
b		**b**	**b**	b	**b**	**b**
c			**c**	c		
d+e				i	**j**	
i					j	
j						

Table 4. Comparison of height distributions of *Nasutitermes corniger* nests among sites in Trinidad & Tobago. Sites (a-e) are mixed broadleaf forest. Site (f) is a dry forest. Site (g) is a mangrove forest. Site (h) is a rubber plantation. Sites (j-k) are farmland. Where two sites differ significantly in median height, the site with the greater median is indicated in the cell.

	b	c	d+e	f	g	h	j	k
a			a	a	a	h	a	a
b			b	b	b		b	b
c			c	c	c	h	c	c
d+e				d+e		h	j	d+e
f						h	j	
g						h	j	g
h							h	h
j								j

However, three *M. arboreus* nests gave evidence of having been in that position from the outset. Each was in the form of a high-domed, radially-symmetrical mound. Dissection of two of these nests revealed no significant structural difference from nests on the sides of trees or rocks.

We confirm the observation by Bennett (1964) and Vesey-Fitzgerald (1939) that the anthophorid bee *Centris derasa* frequently nests in active *M. arboreus* nests and apparently nowhere else at any of our sites.

A notable feature of *N. ephratae* nests is their frequent placement around relatively thin tree trunks or large vines, in contrast to *N. corniger*'s tendency to nest on the side of more massive trunks and branches. It is not rare to find a substantial *N. ephratae* nest based on a tree little beyond the sapling

Table 5. Nest weight and estimated composition of 21 *Microcerotermes arboreus* colonies, extrapolated from samples of about 25 g from each nest.

Weight (kg)	Total adults	Workers	Soldiers	Alates	Soldiers (%)
0.16	2,824	2,777	46	0	1.7
0.32	6,393	6,190	202	0	3.2
0.50	6,001	5,860	141	0	2.4
0.67	10,538	10,305	232	0	2.2
0.72	10,908	10,456	451	0	4.1
0.79	10,881	10,634	247	0	2.3
0.87	37,061	36,048	1013	0	2.7
0.99	5,550	5,471	79	0	1.4
1.00	9,146	9,014	131	0	1.4
1.00	15,390	15,059	330	0	2.2
1.34	15,581	15,037	544	0	3.5
1.46	17,732	17,285	447	0	2.5
1.63	34,797	33,848	949	0	2.7
1.78	17,669	17,287	328	0	2.2
2.01	65,720	63,635	2085	0	3.2
2.13	38,536	37,261	1274	0	3.3
2.17	32,076	31,343	732	0	2.3
2.38	26,469	25,908	560	0	2.1
2.63	36,061	34,808	1253	0	3.5
3.01	30,043	29,479	564	0	1.9
4.20	142,633	138,975	3675	0	2.6

stage, and we repeatedly found very small trees bowed down by the weight of such nests, sometimes such that the nest rested on the ground. Inasmuch as *N. ephratae* nests appear to reach significantly greater size in Trinidad & Tobago than the largest *N. corniger* nests, this difference in nesting habit was unexpected.

Tables 5-7 give nest weights and estimated colony compositions in each species. In *M. arboreus* and *N. corniger*, colony size -- expressed as the total number of adults -- is positively correlated with nest weight over almost a 30-fold weight range (Pearson's $r \geq 0.72$ in each species, $p<0.001$). In our smaller sample of *N. ephratae* colonies, the correlation is weaker ($r=0.63$, $p=0.067$).

Workers made up the bulk of adult termites in each species, while we found alate reproductives only in one *N. corniger* nest. Differences in colony composition are most apparent in the fraction of soldiers. *N. corniger* and *N. ephratae* had very similar mean soldier fractions of 17.4% and 16.5%, respectively. In contrast, in *M. arboreus* only 2.8% of adults were soldiers.

Table 6. Nest weight and estimated composition of 21 *Nasutitermes corniger* colonies, extrapolated from samples of about 25 g from each nest.

Weight (kg)	Total adults	Workers	Soldiers	Alates	Soldiers (%)
0.13	8,934	7,232	1,702	0	19.2
0.14	10,291	9,058	1,233	0	12.0
0.24	14,177	11,878	2,299	0	16.2
0.38	17,105	14,500	2,605	0	15.5
0.58	13,311	11,456	1,854	0	13.9
0.71	47,485	39,467	8,018	0	16.9
0.81	50,096	41,847	8,249	0	16.5
0.87	41,916	35,619	6,217	0	14.8
0.91	65,559	53,731	11,828	0	18.0
0.96	13,044	11,791	2,807	0	21.5
1.99	43,837	36,817	7,019	0	16.0
2.01	86,663	69,777	16,886	0	19.5
2.01	105,086	84,447	20,639	2646	19.2
2.11	50,090	42,663	7,427	0	14.8
2.11	54,118	43,451	10,667	0	17.8
2.19	30,600	23,468	7,131	0	23.3
2.65	68,132	60,016	8,116	0	12.0
2.98	163,178	132,744	30,431	0	18.6
3.10	175,369	141,942	33,427	0	19.1
3.21	32,139	24,891	7,248	0	22.6
3.88	359,644	290,859	66,155	0	19.1

Table 7. Nest weight and estimated composition of nine *Nasutitermes ephratae* colonies, extrapolated from samples of about 25 g from each nest.

Weight (kg)	Total adults	Workers	Soldiers	Alates	Soldiers (%)
0.24	32,110	27,106	5,003	0	15.6
2.23	249,967	203,092	46,875	0	18.7
2.32	159,631	138,260	22,985	0	14.4
2.60	294,608	250,402	44,205	0	15.0
3.21	93,494	74,796	18,699	0	20.0
3.42	472,099	401,702	70,369	0	17.5
4.56	256,792	227,513	38,624	0	15.0
5.01	624,803	533,329	91,437	0	14.6
6.75	357,642	291,468	66,155	0	18.5

The number of soldiers is very strongly correlated with colony size ($r \geq 0.98$, $p < 0.001$). In no species is soldier fraction significantly correlated with colony size ($|r| \leq 0.20$, $p \geq 0.39$), consistent with the hypothesis that the growing colony maintains a constant proportion of soldiers.

DISCUSSION

It is not surprising that species diversity was much lower, overall, in the more strongly human-disturbed habitats (Table 1). In each of these latter (sites h-k), the fraction of colonies represented by the most abundant species is greater than in any of the more natural habitats (a-g) except for the mangrove forest, with its naturally very low diversity of trees.

Against expectation, we found no overall tendency for one species to nest higher than another. Against this, there are often significant differences in average nest heights among habitats, with all three species apparently varying together.

There are two very large problems in making sense of this pattern. Quite simply, we have virtually no idea of either the ultimate or the proximate causes for nesting at one height rather than another. The wide variance at each site suggests that there can be no very acute advantage in choosing the level at which to nest.

In termites, the choice of a nest site is made by the queen and king moving in tandem after they have lost their wings and formed a pair-bond (Nutting

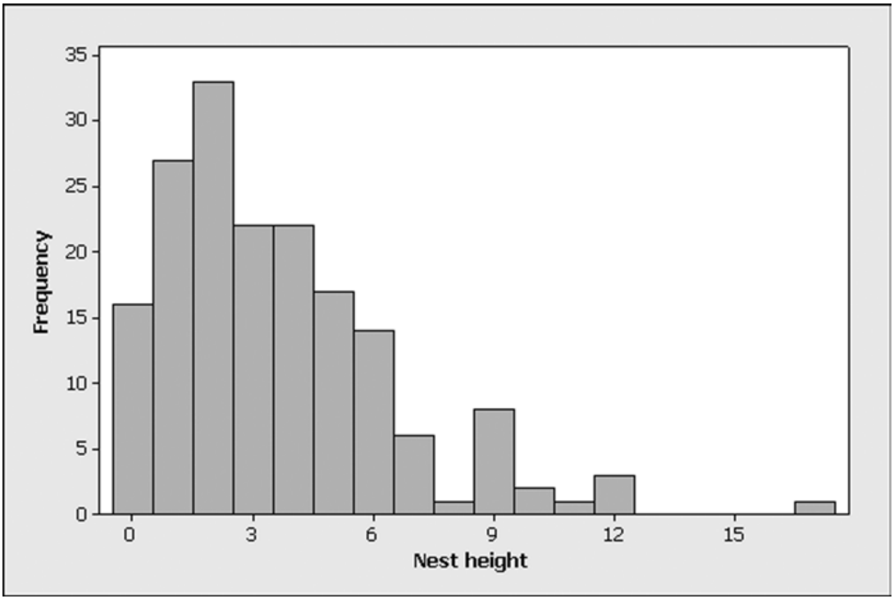

Fig. 1. Height frequency distribution of 173 *Microcerotermes arboreus* nests in mixed broadleaf forest (site a).

1969). Observations of pairing in several termite species that nest in the soil or at ground level indicate that this occurs on the ground or very low vegetation (Grassé 1984: Chapter 3; Nutting 1969). However, in the absence of any knowledge of this process in arboreal termites, it is plausible that alates land directly on tree trunks from their mating flights, and then pair and burrow into the wood very near the spot. Consistent with this suggestion, most of our height-frequency distributions were distinctly skewed, with modes between one and four meters (Table 2) and a long tail (e.g. Fig. 1).

N. corniger has been characterized as typically polygynous in Jamaica (Clarke 1991) and Antigua (Roisin & Pasteels 1986), but not in Trinidad (Clarke 1991; our observations). It will require larger, more systematic datasets to determine whether there is a geographic and/or habitat pattern in the apparent variation.

Our finding of a mean of 17.4% soldiers among adults of *N. corniger* is similar to Clarke's (1990) finding of means of 13.0% in six main nests and 15.1% in 15 auxiliary nests of this species in Trinidad. Our finding of a very similar soldier fraction in *N. ephratae* is also according to expectation.

The sharp contrast between the fractions of soldiers in the two *Nasutitermes* species and in *M. arboreus*, conforms to the pattern of much higher soldier fractions in nasute-termites than in other higher termites (Haverty 1977). In the species under study, we suggest that this correlates with differences in structure of the exposed nests. Although both *Microcerotermes* and *Nasutitermes* typically make nests of wood carton, those of *Microcerotermes* are considerable more compact (Grassé 1984). Nests of both *Nastutitermes* species show definite structural weaknesses with respect to a macro-predator. In *N. corniger* it is the envelope and outer layers that are brittle and easily broken, while in *N. ephratae* it is the envelope and nest core.

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