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SHORT COMMUNICATION

Nest structure and colony composition of two neotropical mound-building termites (Blattaria: Termitidae: *Nasutitermes coxipoensis* and *Cortaritermes intermedius*)

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Abstract

On the island of Trinidad, West Indies the mound-nesting *Nasutitermes coxipoensus* and *Cortaritermes intermedius* (Nasutitermitinae) are each only known from one distinct savanna habitat. The former builds larger nests that harbour larger colonies. Three common plants were often found growing directly from *C. intermedius* nests. Consistent with what is known from other nasutitermitines, the proportion of soldiers in the colony is high in each species: 11–15% of adults in most *N. coxipoensis* and 7–19% in *C. intermedius* colonies. While this shows no correlation with overall colony size in *N. coxipoensis*, we found a negative correlation between these two parameters in *C. intermedius*. Consistent with what has been found in some mound-nesting fungus-gardening termites (Macrotermitinae), mounds of both species showed a higher concentration of some elements and organic matter than in the surrounding surface soil.

Keywords *Brysonima crassifolia* · *Chrysobalanus icaco* · Colony composition · *Cortaritermes* · *Miconia ciliata* · *Nasutitermes* · Nest structure · Savanna · Soil composition

Trinidad is a continental island off the northeastern corner of the South American mainland. Its biota is broadly harmonious with that of the nearby mainland, showing much the same composition of plant and animal taxa (Starr 2009). Its native climax vegetation is mostly seasonal evergreen forest, although with several substantial pockets of natural savanna (Beard 1946; Comeau 1990; Graf 1961).

Among these are the Erin Savannas near the southern edge of the island and the Aripo Savannas in the north-central part (Fig. 1). The Erin Savannas are in relatively well-drained rolling hills with annual rainfall of about 160 mm, while the Aripo Savannas are much flatter with a poorly-drained clay base and annual rainfall of 250–280 mm. Vegetation of these treeless pockets is dominated by sedges and grasses on mineral soils with little organic matter. The lack of tree cover is not due to low rainfall but to these soil conditions. Although the savannas are subject to sporadic fires (Arneaud et al. 2021), they are not believed to be fire-climaxes (Comeau 1990; Comeau and Clubbe 1998). Comeau (1990: Table III) listed 37 plants from the Erin Savannas, of which 17 were shared with the Aripo Savannas. Included in Comeau's (1990: Table I) list of common plants of the Aripo Savannas are the shrubs *Chrysobalanus icaco* (Rosaceae) and *Brysonima crassifolia* (Malpighiaceae), to which we add the herb *Miconia ciliata* (Melastomataceae).

Nasutitermitinae are a speciose, pantropical subfamily of Termitidae whose most salient shared feature is their distinctive nose-soldiers, or nasutes. Unlike soldiers of many termites, the mandibles of these are much reduced and (as far as we know) non-functional, so that they cannot serve as a defensive armature. Rather, the eyeless head is extended forward into a pointed proboscis from which soldiers can forcefully exude their abundant defensive compounds (Constantino 2021). The proportion of soldiers to workers in the colony varies considerably among termite taxa (Haverty 1977: Table). It is notable that this is consistently high in nasutes-termites. Whole-nest samples from nine species showed a median soldier proportion of 17.3%, none below 10% (Haverty 1977; Merritt and Starr 2010). In contrast,

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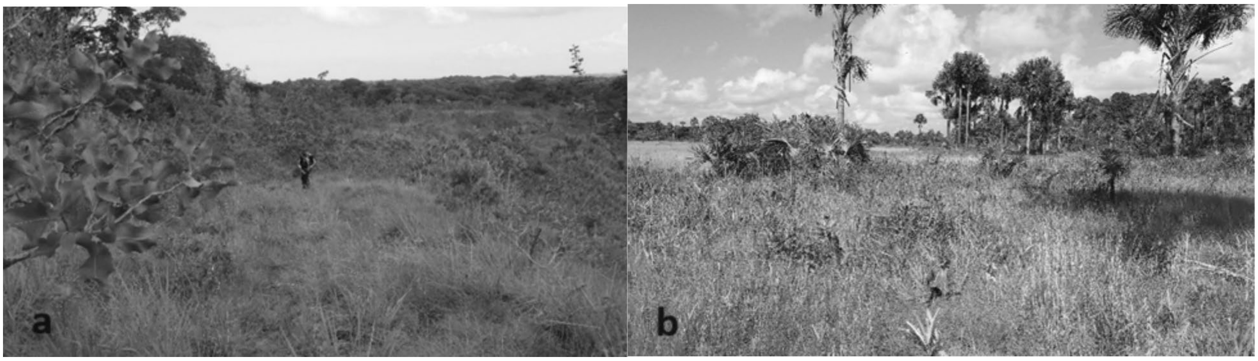

Fig. 1 Habitat views of Erin Savannas (**a**) and Aripo Savannas (**b**), Trinidad

Fig. 2 Intact mound nests of *Nasutitermes coxipoensis* (**a**) and *Cortaritermes intermedius* (**b**). Note typically more regular surface of *N. coxipoensis* nest

Fig. 3 Three plants commonly found growing from *Cortaritermes intermedius* nests in the Aripo Savannas. **a** *Byrsonima crassifolia*. **b** *Chrysobalanus icaco*. c. *Miconia ciliata*

Table 1 Association of three common plants with *Cortaritermes intermedius* mound-nests and apart from nests along a 500-m transect in the Aripo Savannas

	Nest-associated	Not associated
Brysonima crassifolia	6	1
Chrysobalanus icaco	33	4
Miconia ciliata	7	0
Total	46	5

the same authors found a median proportion of 2.5% in 50 non-nasute species, of which only three were as high as 10%.

The known neotropical nasutes-termites comprise 171 species in 31 genera, of which 16 species are found in Trinidad (Scheffrahn et al. 2003). Of these, 13 typically nest on trunks and branches of trees and other above-ground situations, while *Nasutitermes callimorphus* Mathews nests underground (R.H. Scheffrahn, pers. comm.). Our focus here is on the two remaining species. In Trinidad these appear only to build and occupy mound nests on the soil surface in savannas. Both *Nasutitermes coxipoensus* (Holmgren) (Fig. 2a) and *Cortaritermes intermedius* (Banks) (Fig. 2b) are widespread in South America (Constantino 2024). *N. coxipoensus* and many congeners have been the subject of several studies (Laffont et al. 2012 and references therein). In contrast, the nesting biology of *C. intermedius* and its four congeners has received almost no attention. Camacaro et al. (2008) found *Cortaritermes* sp. to be conspicuous in a well-drained savanna in Venezuela, with a density of 633 active nests/ha. Treating the nest as hemispherical, Laffont et al. (2012) found very wide size variation in 41 nests of *N. coxipoensus*, with a median volume of 30 L. The nests had an approximately homogeneous cellular structure (Laffont et al. 2012). Torales et al. (2006) reported colony sizes ranging from 4693 to 77,180 (mean = 28,873) individuals. They found no correlation between nest volume and colony size. This is in contrast to the result of a meta-analysis of data from 24 species of mound-building termites (Josens and Soki 2010), which yielded the expected positive relationship between the two parameters.

Table 2 Nest dimensions of *Nasutitermes coxipoensis* and *Cortaritermes intermedius*

Nest no	Height above ground (cm)	Depth below ground (cm)	Width at ground level (cm)	Volume (l)
N. coxipoensis				
1	25	9	30	16.0
2	23.5	8	33	18.0
3	37	8	31	22.6
4	27	8	34	21.1
5	26	9	32	18.7
C. intermedius				
1	17	26	6.0	
2	20	21.5	4.8	
3	19	22.5	5.0	
4	13.5	31	6.8	
5	15.5	26	5.5	

Those of *C. intermedius* hardly extended down into the soil, so that depth is disregarded

Table 3 Colony composition of *Nasutitermes coxipoensis* and *Cortaritermes intermedius*

Nest no	Workers	Soldiers	Total adults	% Soldiers (range)
N. coxipoensis				
1	25,251	3146	28,397	11.1 (10.5–11.7)
2	16,282	2929	19,211	15.2 (13.5–17.0)
3	47,640	7913	55,553	14.2 (11.5–17.5)
4	32,665	9006	41,671	21.6 (21.5–21.8)
5	23,320	4161	27,481	15.1 (14.9–15.4)
C. intermedius				
1	15,686	1131	16,817	6.7 (6.5–6.9)
2	3938	940	4878	19.3 (18.8–20.0)
3	9148	920	10,068	9.1 (7.6–10.2)
4	5774	1334	7108	18.9 (14.5–26.0)
5	8505	1115	9620	11.6 (7.6–28.8)

Numbers of workers and soldiers in each colony are extrapolated from the pooled nest subsamples according to subsample and whole-nest weight. The estimated percentage of soldiers in each colony is followed by the range in the subsamples

Tropical savanna soils are characterized by minimal weathering, low humus content and poor crumb structure (Bourlière 1983). These soils are typically associated with flat landscapes (Beard 1953; Bourlière 1983; Richardson 1963), as in the Aripo Savannas. Natural drainage and topography are recognized as critical factors influencing the development of tropical soils (Ahmed et al. 2019; Beard 1953). Recent research suggests a positive correlation between the long-term activity of termites and increased fertility in tropical soils (Bruand et al. 2023).

Mound-building termites can have a substantial effect on soil profiles through tunneling that promotes the mixing of soil layers, selective transport of soil particles for nest construction, and concentration of organic matter in the mound (Fernandes et al. 2018; Holt and Lepage 2000; Lobryn-de-Bruyn and Comacher 1990). As a result, farmers in some tropical regions have treated mound soil as a form of fertilizer (Black and Okwakol 1997; López-Hernández 2023; Wood 1996). Since the pioneering work of Lee and Wood (1971), it has been recognized that some plants are mostly found growing on termite mounds (e.g. Joseph et al. 2012).

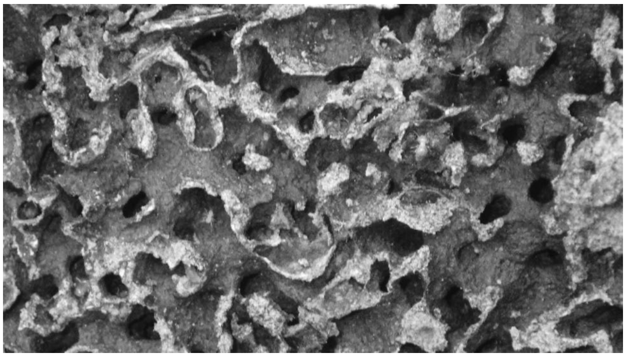

Fig. 4 Internal matrix of *Cortaritermes intermedius* nest

Most studies of termite mound-nests in this respect have treated the Old World tropical fungus-gardening Macrotermitinae. Here we treat two species of a different subfamily, most of whose members do not make mound nests.

We did field studies in March (*C. intermedius*) and April 2023 (*N. cortaritermes*) during the early-mid dry season. Identification of species was somewhat indirect, as legal restrictions within Brazil prevented sending specimens to a specialist, Reginaldo Constantino at the University of Brasília. However, an exchange of photos and examination under Dr Constantino's direction led to the definite identification of *N. coxipoensis* and the conclusion that the other species is most likely *C. intermedius*.

To assess the relationship between *C. intermedius* mounds and the three above-mentioned plants mentioned that often grow from them in the Aripo Savannas, one of us (LA) walked a single transect of about 500 m, recording the incidence of any of the three plants growing from the first 50 mounds (whether apparently active or not) encountered, as well as any of those plants apart from any mound within a meter of the transect line. In those few cases where more than one of these plants grew on a mound, we recorded only the predominant species assessed by relative size or, where necessary, by means of the root collar diameter (RCD).

Identifying five apparently typical active mounds of each species, we took structural notes on each while intact and opened. We recorded mound height, width at ground level, and underground depth. To estimate nest volume in liters, we treated each *C. intermedius* mound as an ellipsoidal dome with maximum width at ground level (Spike's Calculators 2024), disregarding the very slight extension down into the soil. Because *N. coxipoensis*'s significant subsoil component, we treated the mound as a double ellipsoidal dome, summing the two.

During the late morning, we collected these 10 nests for transport to the lab. Following the method of Merritt and Starr (2010), we froze the nest overnight to kill all termites. After thawing the nest for at least two hours, we broke it into very small fragments, homogenized it by stirring, and extracted and weighed three samples of about 25 g each. From these, we recorded numbers of workers and soldiers, as well as any pre-alates and alates. This allowed an estimate by extrapolation of whole-colony composition.

We collected 20 soil samples of about 2 kg, 10 from each site. These comprised a sample from each of the five mound nests and a surface sample from about one meter away from the mound. Samples were analyzed by Agro Services International Inc. of Orange City, Florida, USA. All analyses followed the systematic approach of Portch and Hunter's (2002) soil fertility evaluation. Exchangeable cations calcium (Ca) and magnesium (Mg) were determined by Atomic Absorption Spectrometry. Extractable sulfur (S) was determined by turbidimetry using the barium chloride method, whereas available boron (B) was determined by colorimetry using the curcumin technique. Total CEC (cation exchange capacity) was determined by summation of exchangeable cations methodology. Available phosphorus (P), potassium (K), iron (Fe), manganese (Mn), zinc (Zn), and copper (Cu), were analyzed via a modified Olsen sodium bicarbonate/EDTA extractant method. Organic matter (OM) and organic carbon (OC) were analyzed using the loss on ignition (LOI) method in a Thermolyne 1400 furnace. Soluble salt (Sol Salt) followed the 1:2 suspension in water method, while active acidity (AA) was determined using 1.0 M KCl titrated with 0.01 M NaOH. Base saturation (Base Satn) was calculated by dividing the total bases by the CEC and multiplying by 100. A Milwaukee Mi150 pH meter (calibrated with standards traceable to NIST SRM 186, 191 standards) was used to measure hydrogen ion (mol/L) concentration.

The Generalized Linear Model (GENLIN) (IBM Corp. 2024) was used to test for differences between termite nest soil and surrounding soil chemical properties. The models used chemical responses as dependent variables and soil type (termite and surrounding) as independent variables. The analyses used linear, gamma, Poisson and negative binomial distributions and linear or log linked functions. Where significant differences were observed, Fisher's Least Significant Difference (LSD) tests were used to identify which factor(s) were responsible for statistical differences.

While the surface vegetation at each site mostly comprises grasses and sedges (Fig. 1), in the Aripo Savannas we also found the low shrubs *Byrsonima crassifolia* (Fig. 3a) and *Chrysobalanus icaco* (Fig. 3b) the herb *Miconia ciliata* (Fig. 3b) associated with *Cortaritermes intermedius* nest mounds. *C. icaco*, in particular, was commonly found growing out of mounds. Of the 50 mounds recorded on the transect, 46 had one or another of these three plants growing from it (Table 1). We recorded just one *B. crassifolia* plant and four *C. icaco* growing apart from any *C. intermedius* nest within one meter of the transect.

Unlike what is reported from some other mound-nesting termites, nests of these two species are not especially hard

Table 4 Mean values for chemical parameters of mound nests and surrounding surface soil in the Erin Savannas (*Nasutitermes coxipoensis*) and Aripo Savannas (*Cortaritermes intermedius*) of Trinidad, West Indies

Parameter	Erin Savannas		Aripo Savannas	
	Mound soil	Surrounding soil	Mound soil	Surrounding soil
Ca meq/100 cm^3	12.38 ± 0.18^a	11.79 ± 0.18^a	4.26 ± 0.16^b	4.72 ± 1.97^b
Mg meq/100 cm^3	$*1.07 \pm 0.06^a$	0.58 ± 0.10^b	$*1.67 \pm 0.15^c$	0.23 ± 0.07^d
K meq/100 cm^3	$*0.47 \pm 0.10^a$	0.20 ± 0.07^b	$*0.40 \pm 0.06^a$	0.02 ± 0.00^b
P µg/cm^3	$*15.60 \pm 5.84^a$	8.60 ± 3.93^a	$*27.00 \pm 5.66^b$	4.00 ± 0.71^c
S meq/100 cm^3	30.80 ± 13.24^a	21.20 ± 6.01^a	9.80 ± 2.69^b	5.00 ± 1.05^b
B meq/100 cm^3	3.75 ± 1.15^a	2.53 ± 0.58^a	$*1.57 \pm 0.45^b$	5.15 ± 3.39^c
Cu meq/100 cm^3	1.00 ± 0.22^a	1.02 ± 0.13^a	1.30 ± 0.26^a	1.28 ± 0.25^a
Fe meq/100 cm^3	181.20 ± 28.12^a	209.40 ± 68.81^a	80.00 ± 36.91^b	58.20 ± 15.07^b
Mn meq/100 cm^3	$*16.88 \pm 5.84^a$	2.98 ± 1.96^b	$*13.64 \pm 3.63^a$	0.50 ± 0.07^c
Zn meq/100 cm^3	$*3.18 \pm 0.86^a$	1.00 ± 0.41^b	$*3.76 \pm 0.46^a$	0.42 ± 0.07^c
CEC meq/100 cm3	33.86 ± 2.16^a	29.68 ± 4.37^a	7.32 ± 0.47^b	8.80 ± 5.58^b
Sol salts ppm	111.80 ± 18.71^a	106.00 ± 45.90^a	175.80 ± 16.22^a	121.90 ± 88.03^a
OM %	$*10.34 \pm 2.34^a$	4.50 ± 2.15^b	$*14.60 \pm 2.43^a$	1.40 ± 0.30^c
OC %	$*6.01 \pm 1.35^a$	2.62 ± 1.25^b	$*8.49 \pm 1.42^a$	0.81 ± 0.17^c
A.A	19.96 ± 2.06^a	17.00 ± 4.28^a	0.98 ± 0.26^b	3.82 ± 3.67^b
Base satn. %	42.60 ± 2.89^a	50.20 ± 12.47^a	87.60 ± 3.23^b	85.00 ± 11.16^b
pH	4.96 ± 0.18^a	5.48 ± 0.34^a	5.40 ± 0.23^a	6.08 ± 0.40^a

Parameters: calcium (Ca), magnesium (Mg), potassium (K), phosphorous (P), sulphur (S), boron (B), copper (Cu), iron (Fe), manganese (Mn), zinc (Zn), cation exchange capacity (CEC), soluble salts (Sol salts), organic matter (OM), organic carbon (OC), active acidity (A.A), base saturation (Base Satn.) and potential of hydrogen (pH). Figures are mean ± SE for five samples. An asterisk indicates a significant different ($p < 0.05$) between mound soil and that of the surrounding savanna. Within each parameter, means with the same superscripted letter are not significantly different from each other

or compact. It was not difficult to dig into any of them with an ordinary garden trowel.

As seen in Fig. 2a, *N. coxipoensis*'s nest formed a neat round mound much like that figured by Laffont et al. (2012: Fig. 1). In contrast, *C. intermedius* nests are less regular and formed of markedly darker material (Fig. 2b). We found no correlation between nest volume (Table 2) and colony size (total workers + soldiers) (Table 3), either in *N. coxipoensis* (Spearman rank correlation test, $r = 0.3$, $p = 0.62$) or *C. intermedius* ($r = 0.2$, $p = 0.75$). We examined the internal structure of the nests only cursorily. The internal matrix in each species resembled that of other nasutitermitines (Fig. 4), including arboreal species. In four opened nests of each species we were able to locate the physogastric queen. In each case, she was about 2–4 cm above the soil surface level. In no case was she surrounded by a distinct royal cell, although the matrix walls around her were somewhat thicker than in most of the nest. We did not find alates in any nest.

Soldier fraction was relatively constant in *N. coxipoensis* across almost a three-fold range of colony size; in four of five colonies it was in the range of 11–15% (Table 3), with no significant correlation between the two parameters ($r = 0.2$, $p = 0.75$). In contrast, *C. intermedius* showed considerable variation across more than a three-fold range of colony sizes. Furthermore, there was a perfect negative correlation between these two measures across our five colonies ($r = -1$, $p = 0.02$).

The absence of a correlation between mound size and colony size may be an artefact of modest sample size. However, our results are consistent with the view that mound size is not very closely tied to colony size (Table 2 and 3).

The high proportion of soldiers in both species is consistent with earlier results from other nasutitermitines, as is the lack of an apparent correlation between this proportion and overall colony size in *N. coxipoensis*. In contrast, the negative correlation between soldier proportion and overall colony size in *C. intermedius* is novel. If this is not an artefact of a small sample size (five colonies), it suggests that in its particular environmental conditions *C. intermedius* colonies can defend themselves with a smaller proportional investment in soldiers as they grow.

There were significant differences in chemical composition between surrounding soils in the two savannas: all parameters except K, Cu, Sol salts and pH (Table 4) (GLiM, x^2, $p < 0.05$). Surrounding soils in the Erin Savannas showed at least twice the concentration of Ca, Mg, P, S, Fe, Mn, ZN, CEC, OM, OC, and A.A), while B, Cu, soluble salts, base saturation and pH were higher in the Aripo Savannas. These are consistent with findings from some fungus-gardening termites of a concentration of some nutrients in mound nests. This may account in the main for the observation that

C. intermedius mounds serve as a frequent substrate for some plants in the Aripo Savannas. However, a plausible additional factor is the mounds' greater porosity and elevation above the flat surrounding soil. In contrast, we observed no tendency for any particular plants to grow out of *N. coxipoensis* mounds in the Erin Savannas.

While our results and those of Arneaud (2020) must be seen as preliminary in this regard, they suggest a role for termite mound nests in influencing vegetation in the two savannas through effects on soil chemical composition).

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Author contributions AM motivated and led the project. CKS designed and directed the study of nest structure and colony composition. LA led the study of nest soil composition. All authors collaborated in the field and laboratory and in preparing the paper.

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