Nest Architecture, Colony Composition and Feeding Substrates of *Nasutitermes coxipoensis* (Isoptera, Termitidae, Nasutitermitinae) in Subtropical Biomes of Northeastern Argentina

by

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ABSTRACT

The mound- building termite *Nasutitermes coxipoensis* is commonly found at subtropical environments of northeast Argentina. This study gives new data about its nest architecture, biology and nutritional habits, comparing these results with other populations of the species. The volume of the analyzed nests varied between 0.91 dm^3 y 207.33 dm^3, a wider range than previously reported for *N. coxipoensis*. The external and internal characteristics of the nests were similar to descriptions from other sites although it was not possible to differentiate the royal cell. The societies were monogynic and the queens laid eggs throughout the year. The body length and weight of primary reproductives were reported. The presence of alates within the mounds was higher in October and November. Feeding substrates consumed by *N. coxipoensis* at these habitats are also reported.

Key words: Isoptera, Termitidae, *Nasutitermes*, Argentina.

INTRODUCTION

Nasutitermes coxipoensis (Holmgren) is a mound- building termite widely distributed in the Neotropical region, cited from French Guyana, Brazil and Argentina (Constantino 2012). Previous field studies on its biology correspond to populations located in savannas of French Guyana (Lefeuve 1987), in the regions of Brazilian Campos and Cerrado (Mathews 1977, Buschini 1996, Garcia *et al.*, 2006, Buschini *et al.* 2008) and the province of Corrientes, Argentina (Torales *et al.* 2006).

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Other authors have reviewed taxonomic (Silvestri 1903, Holmgren 1910, Mathews 1977), morpho-anatomic (Xavier Soares & Costa Leonardo 2002, Buschini & Costa Leonardo 2002) and histological aspects of the species (Cunha *et al.* 2009 a y b), as well as its reproductive mechanisms (Lefeuve 1987, Buschini & Costa Leonardo 1999) and analyses of substrates for survival tests (Albuquerque *et al.* 2008).

In some widely distributed termite species, the nest characteristics sometimes show variations due to geographic, climatic or edaphic differences, reflecting intraspecific plasticity in the construction of these structures (Korb & Linsenmair 1998, 1999; Noirot & Darlington 2000, Korb 2010). Also, some species can vary in several life history traits, reproductive strategies or nutritional habits at different zones of its geographical distribution (Leponce *et al.* 1995, Jeyasingh & Fuller 2004, Arango 2007, Lenz *et al.* 2009).

In northeastern Argentina, the populations of *N. coxipoensis* occupy several vegetation units of the Paranaense (Campos District) and Chaco (Chacoan Eastern District) phytogeographical provinces (Torales *et al.* 1997, 2005,

Figure 1. Mound built by *N. coxipoensis*. Note the irregular external surface.

2007, 2008, 2009, Laffont *et al.* 2004). Given the broad distribution of this species, inhabiting different climatic and landscape units in a wide latitudinal range, this study provides new data on the biology, nutritional habits and nest architecture of *N. coxipoensis* in subtropical environments from northeastern Argentina and observations on its population dynamics.

MATERIALS AND METHODS

The study areas were located in three sampling sites at Mburucuyá (28º04'09"S, 58º 15'23" W, Mburucuyá Department) and two sites at Villa Olivari (27°38'01"S, 56º 54'19" W, Ituzaingó Department) of the province of Corrientes, Argentina. The climate is subtropical and the mean annual temperatures oscillate between 21.5ºC and 19.5°C. Rainfalls are irregular, more frequent in autumn and spring but without a noticeable dry season, with annual average of about 1.500- 1.000 mm (Carnevali 1994).

Fig. 2. Internal view of a partially dissected *N. coxipoensis* nest.

At Mburucuyá, the populations of *N. coxipoensis* were located at *Andropogon lateralis* Nees and *Elyonurus muticus* (Spreng.) Kuntze grasslands, as well as in *Paspalum notatum* Flügge pastures with cattle grazing. At Villa Olivari, the nests were found in plantations of exotic trees (*Pinus* sp. and *Eucalyptus grandis* Hill ex Maiden) and sandy dunes with several species of grasses, bordering the banks of the Parana River. In both localities, the *N. coxipoensis* nests were found scattered among the epigeal nests constructed by other Termitidae (*Cornitermes cumulans* Kollar, *Cortaritermes fulviceps* Silvestri or both).

The nest architecture was described based on 41 *N. coxipoensis* termitaria selected from such populations. The arrangement of runways and the castes present in each of these nests were examined in the field and at the labora-

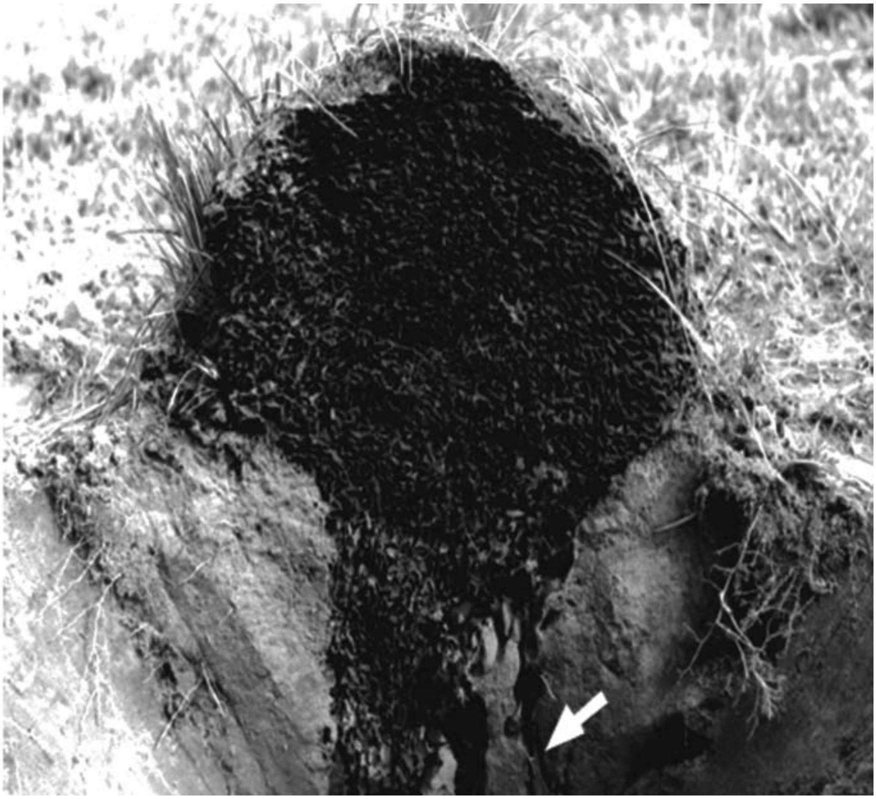

Fig. 3. Section of *N. coxipoensis* nest. Arrow: Lower galleries inside the soil.

tory, applying a modification of the methodology described by Torales *et al.* (2006) to study the qualitative composition of colonies.

The nest volumes were calculated according to the formula used by Buschini & Costa Leonardo (1999), for comparison, assuming the similarity of the nests to a hemisphere. However, since the nests also have a hypogeal sector, the calculated volume is considered only approximate. The depth to which cells spread within the soil profile were also measured.

The total body length (TBL) and wet weight (W) of the reproductives was recorded according to the specimen availability, because some of them were damaged while dissecting the nests. The lengths were measured with a caliper Mitutoyo 530-312, and weights were recorded with a precision balance UWE NJW-150. Photographs were taken with a digital camera Kodak 913 (8.0 Mpx).

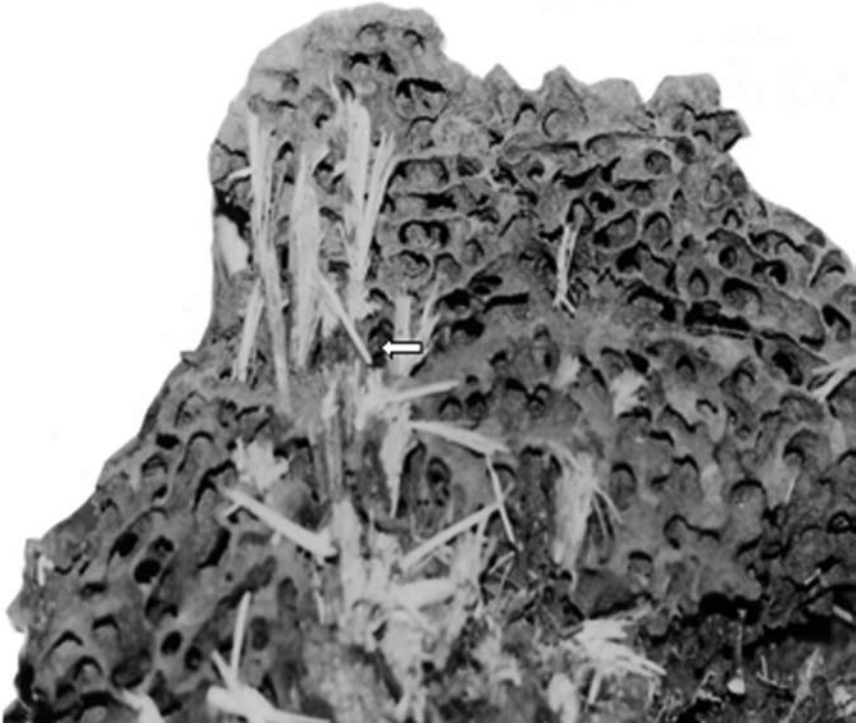

Fig. 4. Detail of the nest chambers (arrow indicates one of the "pillars").

RESULTS AND DISCUSSION

The field observations of *N. coxipoensis* epigeal nests showed that despite some unremarkable variations, the caps were approximately hemispherical, with mean values of 1.39 m (basal diameter), 0.24 m (height) and 0.25 m (depth) (Table 1). A similar morphology is recognized for nests of this species in the Brazilian Cerrado (Buschini *et al.* 2008). These mounds grew slightly deeper in the substrate and its maximum height (0.42 m) was lower than the record of Lefeuve (1987), who reports nests up to 1.00 m in French Guiana savannas.

The volume of the analyzed *N. coxipoensis* nests ranged from 0.91 dm^3 to 207.33 dm^3, with an average of 38.46 dm^3 (Table 1). These values extend the range reported for the species by Lefeuve (1987) and Buschini & Costa Leonardo (1999). Large differences in size between colonies were evident in these populations, such as those from Sao Paulo, Brazil (Buschini & Costa Leonardo 1999). Of the nests analyzed in this study, 65.85% were smaller than the mean volume and in seven of them the volume was less than 9 dm^3.

In the province of Corrientes, *N. coxipoensis* nests have only been detected so far in sandy soils. However, in the Brazilian Cerrado, although the number is higher in this type of soils, they are also located in lateritic surfaces (Mathews 1977, Buschini *et al.* 2008).

Fig. 5. Incipient nest of *N. coxipoensis* with covered runways departing from it.

The outer surface of the nests was irregular, with granular-like protuberances corresponding to protruding internal cells. This surface was constituted by a thin layer (3- 4 mm thick) of fragile sandy consistency, which was easily removed and range in color from light or dark brown to reddish brown (Fig. 1). Unlike the records of Mathews (1977), there were

Table 1. Nest locations, collection date and dimensions, and colony composition of *N. coxipoensis*. D: depth, R: reproductives, E: eggs, L: larvae, Ws: white soldiers, W: workers, S: soldiers, N: nymphs, A: alates, +: present, -: absent or not found.

Nest	Month	Locality	Volume (dm^3)	D	R ♀	♀	E	L	Ws	W	S	N	A
1	Feb	Mburucuyá	28.36	0.25	1	-	+	+	+	+	+	+	-
2	Feb	Mburucuyá	15.83	0.24	1	1	+	+	+	+	+	+	-
3	Feb	Mburucuyá	2.66	0.14	-		-	-	-	+	+	-	-
4	Feb	Mburucuyá	20.37	0.14	-		+	+	+	+	+	-	-
5	Mar	V. Olivari	88.28	0.28	-		-	+	-	+	+	-	-
6	Mar	V. Olivari	30.20	0.26	-		+	+	-	+	+	+	-
7	Mar	V. Olivari	92.94	0.30	-		+	+	-	+	+	+	-
8	Mar	V. Olivari	1.13	0.18	1	-	-	+	+	+	+	-	-
9	Apr	C. Laurel	33.65	0.53	-		+	+	+	+	+	+	-
10	May	S. Antonio	38.78	0.30	-		+	+	-	+	+	+	-
11	Jun	Mburucuyá	15.83	0.30	-		+	+	+	+	+	+	-
12	Jun	Mburucuyá	21.23	0.20	-		+	+	+	+	+	+	-
13	Jun	Mburucuyá	31.36	0.25	1	-	-	+	-	+	+	+	-
14	Jul	V. Olivari	0.91	0.06	-		-	+	-	+	+	-	-
15	Jul	V. Olivari	2.20	0.20	1	1	-	+	-	+	+	-	-
16	Ag	C. Laurel	46.79	0.35	-		+	+	-	+	+	+	-
17	Ag	C. Laurel	23.72	0.21	-		+	+	-	+	+	+	-
18	Ag	V. Olivari	54.82	0.26	-		+	+	-	+	+	+	-
19	Ag	V. Olivari	35.57	0.28	-		+	+	-	+	+	+	-
20	Sep	Ituzaingó	9.39	0.32	-		+	+	-	+	+	-	-
21	Sep	Mburucuyá	7.87	0.12	-		+	+	-	+	+	-	-
22	Sep	Mburucuyá	52.00	0.25	1	-	+	+	+	+	+	+	-
23	Sep	Mburucuyá	12.91	0.20	1	1	+	+	+	+	+	+	-
24	Sep	Mburucuyá	58.41	0.50	1	1	+	+	+	+	+	-	-
25	Oct	C. Laurel	41.76	0.40	-		+	+	+	+	+	-	+
26	Oct	C. Laurel	33.29	0.35	-		-	+	+	+	+	-	+
27	Nov	Mburucuyá	57.10	0.31	-		+	+	+	+	+	+	+
28	Nov	Mburucuyá	18.79	0.26	1	-	+	+	+	+	+	-	+
29	Nov	Mburucuyá	38.61	0.20	-		+	+	+	+	+	-	+
30	Nov	Mburucuyá	39.78	0.25	-		+	+	-	+	+	-	+
31	Nov	Mburucuyá	47.17	0.27	1	-	+	+	+	+	+	-	+
32	Nov	Mburucuyá	20.54	0.20	-		+	+	+	+	+	-	+
33	Nov	Mburucuyá	33.94	0.22	-		+	+	-	+	+	-	+
34	Nov	Mburucuyá	52.25	0.24	-		+	+	+	+	+	-	+
35	Nov	Mburucuyá	12.90	0.17	-		+	+	-	+	+	+	+
36	Nov	Mburucuyá	13.20	0.15	-		-	+	-	+	+	-	-
37	Dic	V. Olivari	207.33	0.30	-		-	-	-	+	+	-	-
38	Dic	V. Olivari	13.71	0.22	-		+	+	+	+	+	-	-
39	Dic	V. Olivari	7.07	0.24	-		+	+	+	+	+	-	-
40	Dic	V. Olivari	8.01	0.18	-		-	+	-	+	+	-	-
41	Dic	V. Olivari	206.21	0.40	-		-	+	+	+	+	+	-

no loose particles of soil covering the mounds. Most nests showed a distinct color contrast between the inner carton (dark brown) and the covering layer (light brown).

The interior of the mounds were made of cardboard-like material (carton), with an approximately homogeneous structure, without remarkable differences between the peripheral and central regions of the nest. The cells were arranged mostly irregularly although several horizontal layers could be recognized in some areas (Fig. 2). The carton used as a building material included partially digested plant debris and sand particles coated with excreta of the workers. The nests had a soft consistency, and are more easily broken than other epigeal termite nests of this region.

Next to the hypogeal sector of the nests, the horizontal strata became discontinuous and the cells took a nearly concentric arrangement around a harder central area. The cells in this core area housed the reproductives and, sometimes, groups of eggs. It was not possible to differentiate the royal cell mentioned by Lefeuve (1987).

Fig. 6. Nest of *N. coxipoensis* and runways on the sandy dunes.

Some cells of different sectors of the nests contained plant debris and/or dry cattle dung possibly transported by workers to the nest, as in other foraging and litter- feeding species where the nests also work as a food reserve site (Thorne *et al.* 1996, Noirot & Darlington 2000). Tunnels of the hypogeal sector continued to the soil depth (Fig. 3).

The walls of all the examined *N. coxipoensis* nests included clumps of grass, as was observed by Mathews (1977) and Lefeuve (1987). Therefore, the cells were distributed between stems and leaves. Some thin stalks were cut into tiny fragments and coated with carton, to be used as reinforcements in the

Fig. 7. *N. coxipoensis* tunnels between grass tussocks.

construction of internal chambers, acting as "pillars" in different layers of cells (Fig. 4). In some nests, two or three layers were bound by the same piece of plant material acting as a column.

In the populations of *N. coxipoensis* located on sandy dunes at Villa Olivari, environmental characteristics allowed us to distinguish clearly the arrangement of numerous covered runways departing from the nests (Fig. 5). There

Fig. 8 a, b. Physogastric queens of *N. coxipoensis*. Bar= 3 mm.

Table 2: Total body length (TBL) and wet weight (W) of primary reproductives of *N. coxipoensis*.

	TBL (mm)				W (g)			
	n	$\bar{x}$	r	s	n	$\bar{x}$	r	s
Females	10	17.4	11.0- 23.0	3.59	6	0.159	0.215- 0.110	0.040
Males	4	6.0	5.0- 7.0	0.81	4	0.012	0.010- 0.015	0.003

were very conspicuous dark tunnels arranged in different directions, on loose light colored sand. Some completely tubular runways stretched to the tussocks of *Panicum* sp., probably one of the main nutrient sources in the dune for *N. coxipoensis* (Fig. 6). The maximum lengths of these runways were 3.20 m for those between two nests, 3.70 m from a nest to a *Panicum* clump and 2.50 m between two clumps of these grasses. These runways were occupied by foraging groups of workers and soldiers. The connections through tunnels between nests and between mounds and grass tussocks, previously recorded for this species (Mathews 1977, Lefeuve 1987) were also observed in Villa Olivari. Furthermore, tunnels linking together grass plants were registered, indicating movement of the groups between them during foraging activity (Fig. 7).

The analysis of the qualitative composition of *N. coxipoensis* societies (Table 1) showed that the colonies in which reproductives were found (10) were monogynous, with primary reproductives located in the core region or central area of the nests. These observations support the fact that *N. coxipoensis* societies have a single royal couple, as has been reported for other populations (Lefeuve 1987, Buschini & Costa Leonardo 1999, Torales *et al.* 2006). These data do not exclude the possibility that, at least sometimes, the colonies are capable of producing multiple reproductives as in several species of *Nasutitermes* (Noirot 1956, Thorne 1982, Thorne & Noirot 1982, Thorne 1984, Roisin & Pastels 1986, Atkinson & Adams 1997, Roisin 2000, Hartke & Baer 2011).

Experimentally, it has been shown that *N. coxipoensis* colonies are able to replace the primary reproductives through replacement individuals (adultoids) within relatively short time, involving a small number of third instar nymphs (Lefeuve 1987). However, this author does not rule out the possibility that replacement sexuates could be originate from alates that remain in the nest after swarming. Replacement reproductives were not found in this study.

The total body length (TBL) and wet weight (W) of reproductives of both sexes are presented in Table 2. All primary female reproductives detected showed varying degrees of fisogastry, with higher LTC values than males (Fig. 8 a, b). Comparatively, the queens of *N. coxipoensis* analyzed in this study showed similar weight to the specimens from French Guyana ($\bar{x}$ = 0.144 g, Lefeuve 1987) but higher than those from the Brazilian Cerrado ($\bar{x}$ = 0.071 g, Buschini & Costa Leonardo 1999). For kings, the individual weight and the mean value were similar to those of Brazil (Buschini & Costa Leonardo 1999).

Under the environmental conditions of this survey, it was observed that queens of *N. coxipoensis* were capable of laying eggs during the four seasons although eggs were not detected in all nests analyzed at each month. In spring, 77% of the nests contained numerous eggs, so it would seem the most favorable period for oviposition. Such observations are supported by the presence of larvae in 95% of the nests from February to December, with

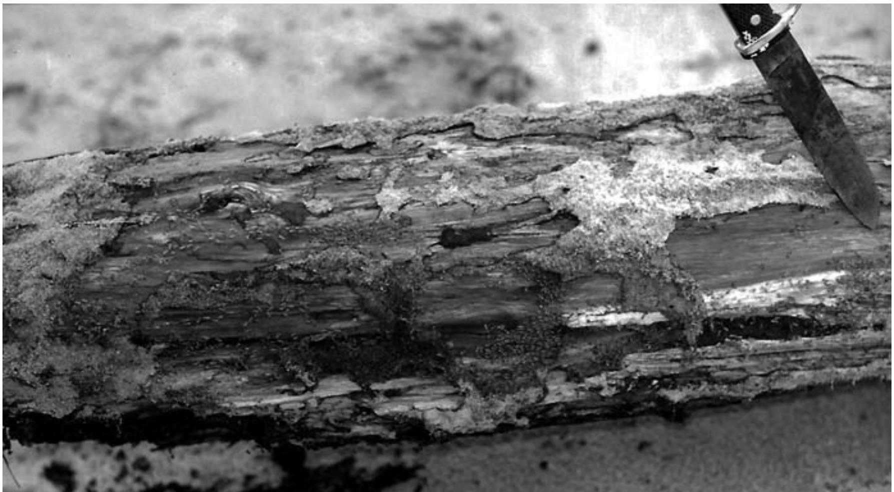

Fig. 9. Piece of dead wood partially excavated by *N. coxipoensis.*

predominance of the first instars ones during spring and summer. The continuous presence of larvae throughout the year confirms our previous records (Torales *et al.* 2006).

White soldiers were detected more frequently in nests examined during the warmer months (September to February: 53.8% of nests) than in the cold season (March-August: 26.6% of nests).

The nymphs were registered in 65% of nests in autumn and winter, declining sharply between September and December (22.7% of colonies). The simultaneous presence of nymphs and alates was only detected in two of the 41 examined nests.

In October and November, 91.6% of the nests contained numerous alates, located in cells near the nest core. During the dissection of the mounds, most of them did not attempt to fly, despite the fact that their wing development seemed to be complete, but tried to hide into the nest. During December, no alates were found inside the mounds, which would confirm that spring is the season when swarming occurs in *N. coxipoensis* as well as in other Termitidae in the province of Corrientes (Torales *et al.* 1999, 2006, Coronel *et al.* 2001,

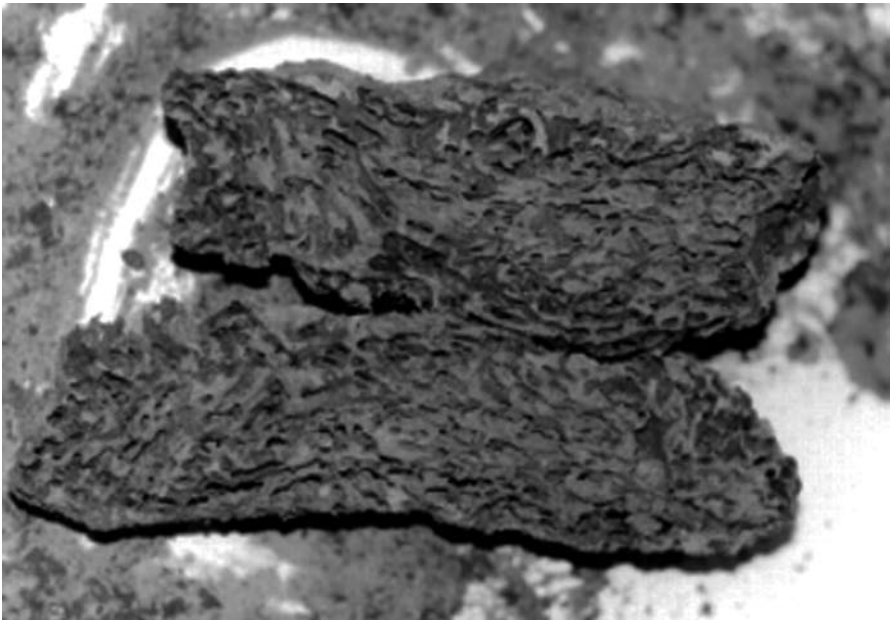

Fig. 10. Longitudinal section of dry cow dung, invaded by *N. coxipoensis*.

Torales & Coronel 2004,). Alates are probably released once a year. In *N. coxipoensis* colonies from French Guyana, the alates are in the nest between October and March and the flights take place from March to May (Lefeuve 1987).

With respect to the feeding substrates consumed by *N. coxipoensis*, stems and roots of grasses partially excavated and colonized by workers and soldiers were frequently observed at all sampling sites in both locations. It was also found that *N. coxipoensis* consumed dead wood from trunks and branches of *Eucalyptus grandis*. The termites deeply excavated the lower surface of the pieces of wood, partially covering those areas (Fig. 9). Grass and dead wood seem to be the main nutrient sources of *N. coxipoensis* in the studied areas, as previously registered in Brazil (Mathews 1977) and this region (Torales *et al.* 2009).

Another resource exploited by *N. coxipoensis* was dry cattle dung. The foraging groups of workers and soldiers were detected in cattle grazing areas, where the masses of manure were thoroughly excavated in the bottom surface contacting the soil, generating cells and galleries occupied by workers and soldiers (Fig. 10). For the construction of these cells, the workers used their feces mixed with plant fibers included in the cattle manure or a mixture of sand and these fibers. The addition of dry cattle dung to their diet increases the exploitation of available food for the species within these habitats. This species was also recorded feeding on dung in the Cerrado (Freyman *et al.* 2008). In addition, the workers of *N. coxipoensis* are able to forage in the open at night (Mathews 1977) and invade living trees in *E. grandis* forest plantations (Laffont *et al.* 1998). In laboratory bioassays, the consumption of sugar cane and paper kraft by *N. coxipoensis* was also registered (Albuquerque *et al.* 2008).

The results reported here allow more detailed descriptions of *N. coxipoensis* nests and expand their recorded volumes. Also, the periods of alate presence and oviposition of queens in the region were reported. The type and number of reproductives agreed with previous observations for this species. Moreover, the substrates consumed in natural and anthropogenic environments of northeastern Argentina revealed a wider feeding plasticity than previously known in this region for *N. coxipoensis.*

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REFERENCES

Albuquerque, A.C., F.M. Cunha, M.A. Oliveira, A.F. Veiga & E.A. Luna-Alves Lima. 2008. Análise de sustratos para testes de sobrevivéncia com *Nasutitermes coxipoensis* (Holmgren) (Isoptera: Termitidae). Arquivos do Instituto Biologico (Sao Paulo) 75: 529- 532.

Arango, R.A., F. Green & G.R. Esenther. 2007. Seasonal response of feeding, differentiation and growth in the eastern subterranean termite *Reticulitermes flavipes* (Kollar) in Wisconsin. The International Research Group on Wood Protection IRG/WP 07-10604. Stockholm, Sweden : IRG Secretariat, 9 p.

Atkinson, L. & E.S. Adams. 1997. The origins and relatedness of multiple reproductives in colonies of the termite *Nasutitermes corniger.* Proceedings of the Royal Society (B) 264: 1131- 1136.

Buschini, M.L.T. & A.M. Costa Leonardo, 1999. Reproductive mechanisms in a *Nasutitermes* species (Isoptera: Termitidae). Revista Brasileira de Biologia 59 (4): 609- 616.

Buschini, M.L.T. & A.M. Costa Leonardo. 2002. Biometrics studies of caste development in *Nasutitermes coxipoensis* (Isoptera; Termitidae). Sociobiology 40 (2): 465- 477.

Buschini, M.L.T., M.A.P. Abuabara & M. Petrere-Jr. 2008. Mathematical models for Isoptera (Insecta) mound growth. Brazilian Journal of Biology 68 (3): 529- 533.

Carnevali, R. 1994. Fitogeografía de la Provincia de Corrientes. Gob. de la Pcia. de Corrientes e INTA. 324 pp.

Constantino, R. 2012. Online Termite Database. http://www.unb.br/ib/zoo/catalog.html, 28 May 2012.

Coronel, J.M., E.R. Laffont, G.J. Torales & E. Porcel. 2001. Variación estacional en la composición de colonias de *Termes saltans* Wasmann (Isoptera: Termitidae, Termitinae). Facena 17: 3 – 13.

Cunha, F.M., V.W. Teixeira, A.C. Teixeira, A.C. Albuquerque, L.C. Alves & E.A. Lima. 2009 a. Caracterização dos hemocitos de operarios de *Nasutitermes coxipoensis* (Holmgren) (Isoptera: Termitidae) e avaliação hemocitária após parasitismo por *Metarhizium anisopliae*. Neotropical Entomology 38 (2): 293- 297.

Cunha, F.M., V.W. Teixeira, A.C. Teixeira, A.C. Albuquerque, L.M.S. Ribeiro, L.C. Alves & F.A. Brayner. 2009 b. Histologia do canal alimentar de operarios da *Nasutitermes coxipoensis* (Holmgren) (Isoptera: Termitidae). Arquivos do Instituto Biologico (Sao Paulo) 76 (2): 307- 312.

Freyman, B.P., R. Buitenwerf, O. DeSouza & H. Olff. 2008. The importance of termites (Isoptera) for the recycling of herbivore dung in tropical ecosystems: a review. European Journal of Entomology 105: 165- 173.

Garcia, J., K. Mackawa, R. Constantino, T. Matsumoto & T. Miura. 2006. Analysis of the genetic diversity of *Nasutitermes coxipoensis* (Isoptera: Termitidae) in natural fragments of Brazilian Cerrado savanna using AFLP markers. Sociobiology 48 (1): 267- 279.

Hartke, T.R. & B. Baer. 2011. The mating biology of termites: a comparative review. Animal Behaviour 82: 927- 936.

Holmgren, N. 1910. Versuch ciner Monographic der Amerikanische *Eutermes-* Arten. Jahrbüchern Ham. Wiss Anstalt 27(2): 171- 325.

Jeyasingh, P.D. & C.A. Fuller. 2004. Habitat-specific life-history variation in the Caribbean termite Nasutitermes acajutlae (Isoptera: Termitidae). Ecological Entomology 29: 606-613.

Korb, J. 2010. Termite Mound Architecture, from Function to Construction (pp. 349- 373). *In*: D.E. Bignell, Y. Roisin & N. Lo (eds.). Biology of Termites: A Modern Synthesis. Springer Verlag.

Korb, J. & K. Linsenmair. 1998. The effects of temperature on the architecture and distribution of *Macrotermes bellicosus* (Isoptera: Macrotermitinae) mounds in different habitats of a West African Guinea savanna. Insectes Sociaux 45: 51- 65.

Korb, J. & K. Linsenmair. 1999. The architecture of termite mounds: a result of a trade-off between thermoregulation and gas exchange? Behavioral Ecology 10: 312- 316.

Laffont, E.R., G.J. Torales, M.O. Arbino, M.C. Godoy, E. Porcel & J.M. Coronel. 1998. Termites asociadas a *Eucalyptus grandis* Hill ex Maiden en el Noreste de la Provincia de Corrientes (Argentina). Revista de Agricultura 73 (2): 201- 214.

Laffont, E.R., G.J. Torales, J.M. Coronel, M.O. Arbino & M.C. Godoy. 2004. Termite (Insecta, Isoptera) Fauna from National Parks of the Northeast Region of Argentina. Scientia Agricola (61): 665- 670.

Lefeuve, P. 1987. Replacement queens in the Neotropical termite *Nasutitermes coxipoensis*. Insectes Sociaux 34 (1): 10- 19.

Lenz, M., B. Kard, T.A. Evans, J. Mauldin, J. Etheridge & H. Abbey. 2009. Differential use of identical food resources by *Reticulitermes flavipes* (Isoptera: Rhinotermitidae) in two types of habitats. Environmental Entomology 38(1): 35-42.

Leponce, M., Y. Roisin & J.M. Pasteels. 1995. Environmental influences on the arboreal nesting termite community in New Guinean coconut plantations. Environmental Entomology 24: 1442- 1452.

Mathews, A.G. 1977. Studies on termites from the Mato Grosso state, Brazil. Academia Brasileira de Ciencias. Rio de Janeiro. 277 pp.

Noirot, C. 1956. Les sexués de remplacement chez les termites supérieurs (Termitidae). Insectes Sociaux 3: 145- 158.

Noirot, C. & J.P.E.C. Darlington. 2000. Termite nests: architecture, regulation and defence (pp. 121- 140). *In*: T. Abe, D.E. Bignell & M. Higashi (eds). Termites: evolution, sociality, symbioses, ecology. Kluwer. Academic Publishers, Dordrecht, The Netherlands.

Roisin, Y. 2000. Diversity and evolution of caste patterns (pp. 95-119). *In*: T. Abe, D.E. Bignell & M. Higashi (eds.). Termites: evolution, sociality, symbioses, ecology. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Roisin, Y. & J.M. Pasteels. 1986. Reproductive mechanisms in termites: polycalism and polygyny in *Nasutitermes polygynous* and *N. costalis.* Insectes Sociaux 33: 149-167.

Silvestri, F. 1903. Contribuzione alla conoscenza dei Termitidi e Termitofili dell' America Meridionale. Redia 1: 1- 234.

Thorne, B.L. 1982. Polygyny in termites: multiple primary queens in colonies of *Nasutitermes corniger* (Motschulsky) (Isoptera: Termitidae). Insectes Sociaux 29: 102- 107.

Thorne, B.L. 1984. Polygyny in the Neotropical termite *Nasutitermes corniger:* life history consequences of queen mutualism. Behavioral Ecology and Sociobiology 14: 117-136.

Thorne, B.L. & C. Noirot. 1982. Ergatoid reproductives in *Nasutitermes corniger* (Motschulsky) (Isoptera: Termitidae). International Journal of Insect Morphology and Embryology 11: 213- 226.

Thorne, B.L., M.S. Collins & K.A. Bjorndal. 1996. Architecture and nutrient analysis of arboreal carton nests of two neotropical *Nasutitermes* species (Isoptera: Termitidae) with notes on embedded nodules. Florida Entomologist 79: 27- 37.

Torales, G.J. & J.M. Coronel. 2004. Qualitative and quantitative composition of colonies of *Microcerotermes strunckii* (Isoptera: Termitidae). Sociobiology 43 (3): 523- 534.

Torales, G.J., E.R. Laffont, M.O. Arbino & M.C. Godoy. 1997. Primera lista faunística de los isópteros de la Argentina. Revista de la Sociedad Entomológica Argentina 56 (1-4): 43- 51.

Torales, G.J., E.R. Laffont, M.O. Arbino & J.M. Coronel. 1999. Composición de colonias de *Cornitermes cumulans* (Kollar) (Isoptera: Termitidae, Nasutitermitinae) en diferentes épocas del año. Revista de la Sociedad Entomológica Argentina 58 (3-4): 189- 196.

Torales, G.J., E.R. Laffont, M.C. Godoy, J.M. Coronel & M.O. Arbino. 2005. Update on Taxonomy and Distribution of Isoptera from Argentina. Sociobiology 45 (3): 853-886.

Torales, G.J., J.M. Coronel, E.R. Laffont, M.C. Godoy, M.O. Arbino & E.A. Porcel. 2006. Analysis of the Population from *Nasutitermes coxipoensis* Nests (Isoptera: Termitidae, Nasutitermitinae), from a Locality of the Province of Corrientes (Argentina). Sociobiology 48 (1): 223- 236.

Torales, G.J., J.M. Coronel, E.R. Laffont, M.C. Godoy & J.L. Fontana. 2007. Termite (Insecta, Isoptera) faunal composition in natural forests of the humid Chaco (Argentina). Sociobiology 50 (2): 419- 433.

Torales, G.J., J.M. Coronel, M.C. Godoy, E.R. Laffont & V. Romero. 2008. Additions to the Taxonomy and Distribution of Isoptera from Argentina. Sociobiology 51 (1): 31- 47.

Torales, G.J., J.M. Coronel, E.R. Laffont, J.L. Fontana & M.C. Godoy. 2009. Termite associations (Insecta, Isoptera) in natural or semi-natural plant communities from Argentina. Sociobiology 54(2): 383- 437.

Xavier Soares, H. & A.M. Costa Leonardo. 2002. Survey of the leg exocrine glands in termites (Isoptera). Revista Brasileira de Entomologia 46(1): 1- 6.