

OCCURRENCE, BODY MASS AND BIOMASS OF *Syntermes* spp. (ISOPTERA: TERMITIDAE) IN RESERVA DUCKE, CENTRAL AMAZONIA

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ABSTRACT — The leaf-feeding species *Syntermes molestus* and *S. spinosus* are two dominant termite species in Reserva Ducke in Central Amazonia; two other species (*S. aculeosus*, *S. longiceps*) exist in the area. All species except *S. aculeosus* were also found in urban areas. The workers of *S. molestus* and *S. spinosus* have average body dry weights of 4.5 ± 0.2 and 13.1 ± 1.4 mg, and the weight of their soldiers is 8.2 ± 0.2 and 51.0 ± 1.7 mg, respectively. Therefore, *S. spinosus* is among the largest termites of the world. In both species, fresh weight is about 4.7 higher than dry weight (a wider relation than in other termite species). The biomass of both species amounted to about 1 g m^{-2} (dry weight; indirect estimate), which rises previous assessments of the total termite biomass by about 36-45%, to a value of $3.0\text{-}3.5 \text{ g m}^{-2}$.

Key Words: Amazon rain forest, leaf-feeding termites, body mass, biomass

Ocorrência, Massa Corporal e Biomassa de Espécies de *Syntermes* (Isoptera: Termitidae) na Reserva Ducke, Amazônia Central.

RESUMO — As espécies comedoras de folhas *Syntermes molestus* and *S. spinosus* são duas espécies de cupins dominantes na Reserva Ducke na Amazonia Central; duas outras espécies (*S. aculeosus*, *S. longiceps*) existem na área. Todas as espécies (exceto *S. aculeosus*) são encontradas também em áreas urbanas. O peso seco médio do corpo dos operários de *S. molestus* e *S. spinosus* é de $4,5 \pm 0,2$ e $13,1 \pm 1,4$ mg, e dos soldados é de $8,2 \pm 0,2$ and $51,0 \pm 1,7$ mg, respectivamente. Por isto, *S. spinosus* está entre os maiores cupins do mundo. Em ambas espécies, o peso fresco é cerca de 4,7 vezes mais alto que o peso seco (uma proporção maior que em outras espécies de cupins). A biomassa das populações de ambas espécies foi avaliada em cerca de 1 g m^{-2} (peso seco; estimativa indireta), o que eleva estimativas anteriores da biomassa total de térmitas em cerca de 36-45%, a um valor de $3,0\text{-}3,5 \text{ g m}^{-2}$.

Palavras-chaves: Floresta Amazônica, cupins comedores de folhas, massa corporal, biomassa

INTRODUCTION

Body size and mass are important features of an animal species which determine its metabolic performance within allometric relationships (Peters, 1983). On the ecosystem level, individual numbers and body mass allow one to determine the "biomass density" of a species (g m^{-2} , kg ha^{-1}) which is a better indicator of its relative importance in the energetics of the ecosystem than density alone. In spite of the great importance of termite

communities for the cycling of nutrients and energy in tropical rain forests, obtaining reliable estimates of their biomass has so far been impossible because of the dispersed nature of their populations (Martius, 1994). Especially those species which have their nests deep in the soil have very likely been underestimated in previous assessments.

The termite genus *Syntermes* consists of comparatively large species, which live in subterranean or epigeal nests and feed on leaf and grass litter. This genus, of which 23

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species are known, occurs only in South America (Constantino, 1995). *Syntermes* species are the most dominant members of the guild of leaf-feeding termites in South America, and they are very abundant in rainforests (Bandeira 1991). The nests of *Syntermes* species can be totally subterranean, the only visible trace being the nest entrances on the soil surface. Those nests can extend to at least 3 meters depth into the soil, which makes the assessment of their populations very difficult (Emerson, 1938; Constantino, 1995; Mill, 1994 in litt.). I report on the occurrence of several *Syntermes* species and on the body mass and biomass of the two most abundant species in the "Reserva Florestal Adolfo Ducke", a forest reserve near the city of Manaus, in Central Amazonia. I use this information and literature data to estimate the population biomass of the two species.

MATERIAL AND METHODS

Workers, soldiers and alates of termites of the genus *Syntermes* were manually collected between 1991 and 1994 during nocturnal excursions to the Central Amazonian rain forest reserve "Reserva Florestal Adolfo Ducke" and in pitfall traps (soldiers, workers) and light traps (alates) set up in the reserve. All termites were preserved in 70% alcohol and deposited in the Invertebrate Collections of INPA, Manaus. For the determination of individual weight, termites of both species were collected on 20-VII-1994 in the forest; the fresh weight of indi-

vidual termites was determined immediately after transferring them to the laboratory; their dry weight was determined after keeping them at 104°C for four days.

RESULTS AND DISCUSSION

Occurrence. Four *Syntermes* species were found in the Ducke reserve: Two smaller species, *Syntermes molestus* and *S. longiceps*, and two very large species, *S. spinosus* and *S. aculeosus*. Both *S. molestus* and *S. spinosus* are very abundant and are easily encountered at night (only sometimes during daytime) foraging on the forest floor (cf. Apolinário, 1993; *Syntermes spinosus* misidentified as *S. "chaquimayensis"*). The other two species are rare; only one worker and some alates have been recorded of *S. longiceps* in Central Amazonia over several years (Apolinário, 1993; Constantino, 1995; cf. also Tab. 1). *S. molestus* and *S. spinosus* swarm also in urban areas, e.g., in the city of Manaus, where alates have been repeatedly captured in light traps (Tab. 1; Martius unpubl.). Their nests may be found in urban areas where trees provide shadow, e.g., in the park-like secondary vegetation of the INPA campus. The latter species was found nesting in clayey and also in sandy soil (campinarana). *S. longiceps* has also been found swarming at the INPA campus (Tab. 1).

Body mass. For termites, body masses (Tab. 2) of individuals of the worker and soldier castes of *Syntermes molestus* and *S. spinosus* are very high. A worker of *S. molestus* has an average body dry weight of 4.5 ± 0.2 mg, and the soldier weighs on average

Table 1. Occurrence of *Syntermes* species in Central Amazonia

Sample Numbers	Species	Soldiers	Workers	Alates	Locality
MA 0018, MA 0015, TI 030	<i>Syntermes aculeosus</i>	X	X	X	R.Ducke; Trombetas
TI 104, MA 0011	<i>Syntermes longiceps*</i>	--	--	X	R.Ducke; INPA Campus
E2-26, TI 038, TI 112, TI 114, TI 113, TI 048, MA 0025, MA 0026, TI 111, TI 041, TI 051, TI 053, TI 021, TI 022, TI 023, TI 024, TI 025, TI 046, TI 105	<i>Syntermes molestus</i>	X	X	X	R.Ducke, Manaus (urban areas; INPA Campus, Parque Mindú), Reserva km 41
TI 102, ALT 002, TI 036, TI 106, TI 035, TI 107, MA 0017, HÖL1, TI 042, TI 043, TI 055, TI 100, TI 020, TI 010, TI 047, TI 040, TI 054, TI 045, TI 044, TI 103, TI 101, TI 026, TI 029, TI 032 Reserva ZF 3;	<i>Syntermes spinosus</i>	X	X	X	R.Ducke (clayey soil and "campinarana"); Manaus (urban areas; INPA Campus), Rio Trombetas

Table 2. Individual body masses (mg/ind.) and fresh-to-dry-weight ratios of *Syntermes molestus* and *S. spinosus* from the Reserva Florestal Adolfo Ducke, Central Amazonia, Brazil. FW = fresh weight, DW = dry weight.

Sample No.	Species	n	Caste	Average Individual Weight		Standard deviations		
				FW (mg)	DW (mg)	FW	DW	FW/DW
021/22	<i>S.molestus</i>	8x5	Workers	20.5	4.5	1.0	0.2	4.61
021/22	<i>S.molestus</i>	7x5	Soldiers	40.3	8.2	1.9	0.2	4.91
020	<i>S.spinopus</i>	4x2	Workers	66.1	13.1	6.3	1.4	5.04
020	<i>S.spinopus</i>	4x1	Soldiers	218.0	51.0	7.1	1.7	4.28
	Overall							4.72

8.2±0.2 mg, almost twice the weight of the worker. *S. spinosus* workers and soldiers weigh 13.1±1.4 mg and 51.0±1.7 mg, respectively, a fourfold difference between the castes. These termites therefore belong to the largest termites of the world, equal in size and mass to the largest *Macrotermes* spp. of Africa. In contrast, most species in Amazonian rain forests weigh around 1 mg (dry weight; Martius, 1994); many humus-feeding species, e.g., *Anoplotermes banksi* with about 0.3 mg dry mass, weigh much less (Martius & Ribeiro, 1997).

The fact that the body mass of all species in the central Amazonian termite

population spans two orders of magnitude (mass classes of 0.1 mg to tens of mg) is important for the determination of metabolic rates of the termite population (e.g., respiration rate; cf. estimates in Martius, 1994), because it does not allow the use of an average body weight for the termite population.

Individual fresh weight is, on average, 4.72 times the dry weight (range 4.1-5.1), indifferent of the species. The fresh-to-dry-weight ratio found in *Syntermes* spp. is much higher than that found for other species. For example, Martius (1989) found FW = 3·DW in *Nasutitermes macrocephalus*; Wood & Sands (1978) assumed

an average of $FW = 4 \cdot DW$ for termites.

In the lack of data on nests or individual density of both species, two approaches based on different literature values are used to assess the biomass of the populations of both species. One approach ("from colony size" in Tab. 3) uses the estimates of Mill (1984) of nest and individual density of *S. molestus* and *S. spinosus* in terra firme forest on Ilha de Maracá, Roraima State, Northern Brazil. Density (ind. m^{-2}) was calculated from this author's information of nest density (nests ha^{-1}) and number of individuals

per nest. The other estimate ("from foraging activity" in Tab. 3) uses Barbosa's (1993) estimate of the number of foraging groups per transect and the number of individuals per foraging group in both species in Reserva Ducke. This information was used to calculate the number of individuals participating in foraging groups on the soil surface (in ind. m^{-2}). In both estimates, the numeric caste proportions determined by Mill (1982) were used. The original data and the derived estimate of population size are shown in Table 3.

The determined mass of the forag-

Table 3. Estimation of population size of two leaf-feeding *Syntermes* species of Reserva Ducke, Central Amazonia

Species	Soldier	Worker	
Body Weight (mg per individuum and caste, dry weight) [CB]			
<i>S. molestus</i>	8.2 mg	4.5 mg	
<i>S. spinosus</i>	51.0 mg	13.1 mg	
Caste proportion (Mill 1982) [CP]			
<i>S. molestus</i>	17%	83%	
Foraging Activity (BARBOSA 1993) [FA]			
(average number of individuals active on the soil surface at night)			
<i>S. molestus</i>	8.5		
<i>S. spinosus</i>	0.6		
TOTAL	9.1		
Colony Size and Density (MILL 1984) [D]			
	Nests-ha ⁻¹	Ind.·Nest ⁻¹	Ind.·m ²
			[D]
<i>S. molestus</i>	11.2	30 000	33.6
<i>S. spinosus</i>	3.8	37 000	14.1
Estimated Population Size (biomass, mg·m ⁻²)			
		From Colony Size	From Foraging Activity
		[D×CP×CB]	[FA×CP×CB]
<i>S. molestus</i>	Workers	604.4	11.8
	Soldiers	125.5	31.7
	Total	729.9	43.5
<i>S. spinosus</i>	Workers	122.2	5.2
	Soldiers	153.3	6.5
	Total	275.5	11.7
Both Species		1005.4	55.2

^{*} originally misidentified as *S. chaquimayensis* in Barbosa (1993) (cf. Constantino, 1995)

^{**} originally misidentified as *S. solidus* in Mill (1984) (cf. Constantino, 1995)

ing parties (55.2 mg. m⁻²) is only 5.5% of the determined total biomass (1005.4 mg. m⁻²) of these two species (Table 3). This may be a result of the fact that at any given time only part of the colony was active on the surface. In terms of individual numbers, foraging termites (9.1 individuals m⁻²) accounted for 19% of the total termite population (47.7 individuals m⁻²). This value is low when compared with data given in Petersen & Luxton (1982), according to which 70-96% of the individuals of nest-building termites may be found foraging outside the nests. However, as the population estimates are from Ilha de Maracá, and foraging party size was determined in Reserva Ducke, these values may also reflect differences in population size between these sites which are about 1000 km apart.

The calculated biomass of 1 g m⁻² for both populations (Table 3) means that the relatively conservative estimate of total termite biomass given in Martius (1994) of 2.0-2.5 g m⁻² may be raised to 3.0-3.5 g m⁻². This corresponds to a living biomass of 14-17 g m⁻², due to the higher conversion factor found in the present study. Therefore, leaf-feeding *Syntermes* species may account for 36-45% of the total population of termites living on the ground of these forests. Basing estimates of termite populations on evaluations of the upper soil strata only may therefore be insufficient.

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Literature cited

- Apolinário, F. B. 1993. *Composição faunística e hábitos de nidificação de térmitas (Insecta: Isoptera) em floresta de terra firme da Amazônia Central*. Tese de Mestrado, INPA/FUA, Manaus. 72 p.
- Bandeira, A. G. 1991. Térmitas (Insecta: Isoptera) consumidores de liteira na Ilha de Maracá, Roraima. *Acta Amazônica*, 21: 15-23.
- Barbosa, R. I. 1993. Período de forrageamento de duas espécies de *Syntermes* (Isoptera, Termitidae) em uma floresta tropical amazônica e a relação com temperatura e umidade do ar. *Revta. bras. Ent.*, 37(4): 763-767.
- Constantino, R. 1995. Revision of the neotropical genus *Syntermes* Holmgren (Isoptera: Termitidae). *The University of Kansas Science Bulletin*, 55(13): 455-518.
- Emerson, A. E. 1938. Termite nests - a study of the phylogeny of behaviour. *Ecological Monographs*, 8(2): 247-284.
- Martius, C. 1989. *Untersuchungen zur Ökologie des Holzabbaus durch Termiten (Isoptera) in zentralamazonischen Überschwemmungswäldern (Várzea)*. AFRA-Verlag, Frankfurt am Main. 285 p.
- Martius, C. 1994. Diversity and ecology of termites in amazonian forests. *Pedobiologia*, 38: 407-428.
- Martius, C.; Ribeiro, J.A. 1997. Colony popu-

- lations and biomass in nests of the Amazonian forest termite *Anoplotermes banksi* Emerson (Isoptera: Termitidae). *Studies on Neotropical Fauna and Environment*, 31 (2): 82-86
- Mill, A. E. 1982. *Foraging and defensive behaviour in neotropical termites*. Doctoral Dissertation, University of Southampton, Southampton. 264 p.
- Mill, A. E. 1984. Predation by the ponerine ant *Pachycondyla commutata* on termites of the genus *Syntermes* in Amazonian rain forest. *Journal of Natural History*, 18(3): 405-410.
- Peters, R.H. 1983. *The ecological implications of body size*. Cambridge University Press, Cambridge. 329 p.
- Petersen, H.; Luxton, M. 1982. Quantitative ecology of microfungi and animals in soil and litter. A comparative analysis of soil fauna populations and their role in decomposition processes. *Oikos*, 39(3): 285-388.
- Wood, T. G.; Sands, W. A. 1978. The role of termites in ecosystems. In: Brian, M.V. (ed.) *Production ecology of ants and termites*. International Biological Programme 13. Cambridge University Press, Cambridge: 245-292.