

Biomass of *Macrotermes natalensis* in the northern Kruger National Park, South Africa – the Effects of Land Characteristics

by

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ABSTRACT

In order to derive biomass estimates for *Macrotermes natalensis* (Hav.) (Isoptera: Termitidae) in the northern Kruger National Park, a statistical bootstrap procedure was carried out using three databases: body mass, colony population sizes and mound density. Live biomass (excluding king and queen) of *M. natalensis* for small, medium and large mounds was found to be 0.17, 1.40 and 4.16 kg, respectively. Dry/wet body mass ratios were established for workers (23.7%), major soldiers (20.3%), minor soldiers (35.3%), nymphs (17.1%), king (35.4%) and queen (20.8%). Average live and dry biomass (including nymphs; excluding reproductives) for the northern KNP was calculated to be 0.51 kg ha⁻¹ (0.051 g m⁻²) and 0.11 kg ha⁻¹ (0.011 g m⁻²), respectively. Geology, geomorphology, elevation, local relief, soil patterns and annual rainfall were the abiotic factors shown to be most influential in determining termite biomass, either directly or indirectly. Termite biomass is high in undulated areas where the elevation is 250–400 m, where granitic and rhyolitic soils occur, and where annual rainfall is high (650–700 mm) in the context of the region.

INTRODUCTION

Biomass estimations for the Isoptera in the Kruger National Park (KNP) have never been attempted before. In the northern KNP the genus *Macrotermes* Holmgren (Macrotermitinae) is, in order of abundance of colonies, represented by a number of species: *Macrotermes natalensis* (Haviland), *Macrotermes ukuzii* Fuller, *Macrotermes michaelsoni* (Sjöstedt) and *Macrotermes falciger* (Gerstäcker) (Meyer *et al.* 1999). Collins

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(1981a) quantified biomass of *Macrotermes bellicosus* (Smeathman) populations in Nigeria. In Kenya, Darlington (1991) estimated biomass for colonies of *M. michaelsoni*. Other studies in the Afrotropical region include those of Ferrar (1982a) and Eggleton *et al.* (1996). Macrotermitine biomass for the Indo-Malayan region was reviewed by Collins (1989). Holt & Easey (1993) reported on biomass of mound-building termites in an Australian assemblage.

Biomass allows for a more realistic evaluation of the importance of a population of small-bodied organisms in an ecosystem than do other quantitative indicators (Odum 1971). While their numbers may be impressive, the conversion of food into biomass may collectively be insignificant due to diminutive body size. Whether large or small-bodied species dominate energy resources is an open question, although it has been suggested that larger organisms govern energy expenditure more efficiently in most local assemblages (Pagel *et al.* 1991; Eggleton *et al.* 1998). Be that as it may, biomass remains a good indicator of the amount of resources that have been utilized, and hence the degree of influence that a species has in an ecosystem. The hypothesis, formulated on basis of field experience, is that termite biomass differs significantly between land classes and is determined by particular environmental factors. Termites are supported by ecosystem processes most likely to be related to good drainage (Meyer *et al.* 1999).

We have previously quantified mound density (e.g., Meyer *et al.* 1999) and colony populations made up by the different castes and subcastes (Meyer *et al.* 2000), for which significant relationships between mound size and colony size were found. The present study illustrates the biomass contribution of *M. natalensis* to the ecosystem, which is otherwise poorly understood and frequently overlooked and underappreciated. In future, re-surveying could be undertaken to assess trends in biomass oscillation and hence secondary production (turn-over).

Because of polymorphism (Baroni-Urbani *et al.* 1978), biomass estimates per unit area will be derived from the proportions of each caste in the colony, colony size and mound density. Landscapes (Gertenbach 1983) will be treated as a priori functional units for estimating biomass.

METHODS

Study Area

The northern part of the KNP comprises roughly one million hectares, which is about half the size of the park. The study area borders Mozambique on the eastern side, and is located between the Olifants

(24.04°S) and Limpopo Rivers (22.32°S) (Meyer *et al.* 1999), the latter being an international border with Zimbabwe. The area is dominated by *Colophospermum mopane* (Fabaceae: Caesalpinioideae) vegetation (Acocks 1988; Coates Palgrave 1988).

In this study the KNP landscape and land type classifications of Gertenbach (1983) and Venter (1990) were used to evaluate the effects of land characteristics on *M. natalensis* biomass. Landscapes (Gertenbach 1983) are based on associations of geomorphology (topography), soil, vegetation patterns, fauna and climate, while land types (Venter 1990) are classified on the basis of terrain morphological patterns (land units) having unique (catenal) soil and vegetation features. These zonations were digitized and the termite data (mound counts) from the survey transects (Meyer *et al.* 1999) was overlaid using GIS procedures.

Transect Design

At least ten 2 hectare (1 km x 20 m) belt-transects were surveyed on foot in each of the 20 northern landscapes (Gertenbach 1983) during 1995 (Meyer *et al.* 1999). The main criteria for transect placement were accessibility from roads and firebreaks (practicality), an even and wide (systematic) spread across each landscape, and no bias towards any landscape (equivalent number of transects in each, independent of area). Transects were placed in straight lines and different directions. Positional fixes of each transect were taken by GPS for geo-referencing.

Collection, Drying and Mass Determination of Termite Samples

The mass (g) of groups of 100–300 individual termites of each of the worker (across subcastes), major soldier, minor soldier and nymphal (across worker and soldier instars) samples from ten different randomly selected mounds was determined on a microbalance with a closed weighing chamber. The total mass for each group was then divided by the number of termites in the group to obtain mass per individual termite. Breeding males and females (kings and queens) sampled were primary reproductives in single pairs. Oven drying of samples was done at approximately 100°C over a period of 24 hours.

The classification of mounds into small (height: 0.30–1.34 m), medium (1.35–2.59 m) and large (2.60–5.00 m) sizes was adopted from previous studies (e.g., Meyer *et al.* 2000).

Data Management and Statistical Procedures

Data processing and analysis were conducted using SAS (SAS Institute 1989). Confidence intervals were determined at the 95% level, where use was made of the first standard deviation (SE) and two-tailed *t* distribution. A GLM (general linear model) procedure was performed

on dry/wet ratios (least-squares means) of termite body mass.

Data on body mass (Table 1), colony populations (Meyer *et al.* 2000) and mound density (Meyer *et al.* 1999) was used to quantify termite mass within different areas (biomass per hectare). Biomass for small, medium and large mounds (Table 2) was determined by getting the product of first and second level variables (Table 3). By multiplying this product with the level three variables, biomass of *M. natalensis* (excl. king and queen mass) per unit area was obtained (e.g., Fig. 1).

The three databases were bootstrapped (repeated re-sampling with replacement) to 300 observations throughout, before the point of derivation (Table 3). This was done so that at the end of calculations (merging of databases) the variation around the means, which escalates along the calculation path, could be taken into account.

During the bootstrap procedure it was not possible to use computer time of the mainframe processor as the seed for any random number function (generator) available in SAS. This is because the computer time was passed to SAS as an integer, resulting in a seed value that remained constant for some cycles of the bootstrapping. To avoid this, a REXX macro was introduced to generate random numbers under CMS using decimal values of mainframe computer time as the seed (Van der Linde, unpubl.). The random number information thus obtained was then passed to SAS, enabling data selection from appropriate SAS data sets to provide bootstrapped data that was processed further.

Because land data (classification format) was not point data (thus discontinuous), analysis was done in pairwise manner (*t* tests) rather than in ordination space. Biomass between different areas (land classes) was compared, based on caste and mound size. In addition, an analysis of biomass in total was done across castes and mound sizes. Only areas where termites occur – as pointed out by previous studies (Meyer 1997; Meyer *et al.* 1999) – were compared. The probability of the variables (biomass per hectare) differing from each other was determined conservatively and liberally by *probt* and *probnorm* functions (SAS Institute 1990). Bootstrapped means ($n = 300$) and the second standard deviation (SD) – determined from natural log-transformed values – were used to calculate *t*.

Selecting all the land class comparisons, where at least marginal significant differences were shown conservatively, and subsequently consolidating land attributes within areas of high and low termite biomass, matrices of abiotic factors affecting *M. natalensis* were obtained (Appendices 1, 2). Probabilities were determined conservatively in order to minimize Type I errors, and liberally to minimize Type II errors. However, both errors were simultaneously reduced (Zar 1996), because *n* was increased by bootstrapping.

Table 1. Mean wet and dry individual body mass and dry/wet body mass ratios for the different castes of *Macrotermes natalensis* (Hav.), with 95% confidence intervals calculated by using the standard error and two-tailed *t* distribution.

Caste or subcaste	Wet body mass (mg)	Dry body mass (mg)	Dry/wet ratio (%) (from least-squares means)
Worker	13.24 ± 0.79 (<i>n</i> = 10)	3.08 ± 0.36 (<i>n</i> = 9)	23.66 ± 2.92 (<i>n</i> = 9)
Major soldier	69.80 ± 2.27 (<i>n</i> = 10)	14.12 ± 1.15 (<i>n</i> = 9)	20.26 ± 2.92 (<i>n</i> = 9)
Minor soldier	17.18 ± 1.20 (<i>n</i> = 10)	6.13 ± 0.59 (<i>n</i> = 9)	35.27 ± 2.92 (<i>n</i> = 9)
Nymph	4.142 ± 0.736 (<i>n</i> = 8)	0.706 ± 0.112 (<i>n</i> = 7)	17.11 ± 3.52 (<i>n</i> = 7)
King	149.3 ± 234.4 (<i>n</i> = 2)	52.6 ± 50.2 (<i>n</i> = 2)	35.42 ± 34.15 (<i>n</i> = 2)
Queen	7044 ¹ ± 789 (<i>n</i> = 2)	1461 ¹ ± 2025 (<i>n</i> = 2)	20.76 ± 34.15 (<i>n</i> = 2)

¹Queen mass averaged here is *sensu stricto* age dependent

RESULTS

The physogastric queens of these colonies have a body mass that is two orders of magnitude larger than that of the king or the major soldiers (Table 1). Other members of the colonies are lower in body mass than the major soldiers.

Nymphs have the lowest dry/wet body mass ratio, while minor soldiers and the king have the highest ratios (Table 1). Workers, major soldiers and the queen have similar ratios of dry/wet body mass (the last two being the closest), and none differed significantly from each other (Table 4). Nymphs thus have the highest moisture content (82.9%) of all the castes.

The major soldiers have the highest biomass per mound, followed by that of workers, minor soldiers and nymphs (Table 2).

Biomass in Landscapes

Higher biomass occurs in small and medium mounds of the Lebombo North (landscape 31), where rainfall and hence litter is relatively high, than in the Far North (e.g., landscapes 26 and 33), where the influence of these two factors is much reduced (Table 5a, Appendix 1a). It is not

Table 2. Mean caste-based live biomass (kg) for different mound sizes, with 95% confidence intervals calculated using the standard error and the two-tailed *t* distribution.

Caste or subcaste	Small	Medium	Large
Workers	0.042 ± 0.005 (<i>n</i> = 300)	0.272 ± 0.027 (<i>n</i> = 300)	1.682 ± 0.394 (<i>n</i> = 300)
Major soldiers	0.115 ± 0.048 (<i>n</i> = 300)	1.006 ± 0.140 (<i>n</i> = 300)	2.135 ± 0.343 (<i>n</i> = 300)
Minor soldiers	0.010 ± 0.001 (<i>n</i> = 300)	0.096 ± 0.015 (<i>n</i> = 300)	0.211 ± 0.039 (<i>n</i> = 300)
Nymphs	0.001 ± 0.002 (<i>n</i> = 300)	0.022 ± 0.003 (<i>n</i> = 300)	0.135 ± 0.046 (<i>n</i> = 300)
Total	0.168 kg	1.396 kg	4.163 kg

Table 3. Schematic exposition of a three-level bootstrap procedure carried out on source (underived) data.

DATABASE		MOUND SIZE	ORIGINAL DATA SET	BOOTSTRAP LEVEL	REPETITIVE DATA SETS HAVING RANDOMLY SELECTED OBSERVATIONS						BIOGRAPHICAL DESCRIPTION	
BODY MASS (Pres. stud.)	Number of observations:		10 (10 mounds sampled)	FIRST	10	10	10	10	10		Individual termite body mass	
	Number of data sets:	1			2	3	...	300				
	Series of means:	\bar{X}_i			$\bar{X}_\#$	$\bar{X}_\#$...	\bar{X}_{dec}				
COLONY POPULATIONS (Meyer et al., 2000)	Small	3 obs. (whole populations)	16 obs. (eight aliquots per mound)	SECOND	3 obs.	3 obs.	3 obs.	3 obs.	3 obs.		Number of individuals in small mounds	
					1	2	3	...	300			
					\bar{X}_i	$\bar{X}_\#$	$\bar{X}_\#$...	\bar{X}_{dec}			
	Medium	16 obs. (eight aliquots per mound)			16 obs.	16 obs.	16 obs.	16 obs.	16 obs.	16 obs.		Number of individuals in medium mounds
					1	2	3	...	300			
					\bar{X}_i	$\bar{X}_\#$	$\bar{X}_\#$...	\bar{X}_{dec}			
Large	16 obs. (eight aliquots per mound)	16 obs.	16 obs.	16 obs.	16 obs.	16 obs.	16 obs.		Number of individuals in large mounds			
		1	2	3	...	300						
		\bar{X}_i	$\bar{X}_\#$	$\bar{X}_\#$...	\bar{X}_{dec}						
MOUND DENSITY (Meyer, unpubl.)		206 obs. (survey transects)		THIRD	206 obs.	206 obs.	206 obs.	206 obs.	206 obs.		Number of small/medium/large mounds per hectare	
					1	2	3	...	300			
					\bar{X}_i	$\bar{X}_\#$	$\bar{X}_\#$...	\bar{X}_{dec}			

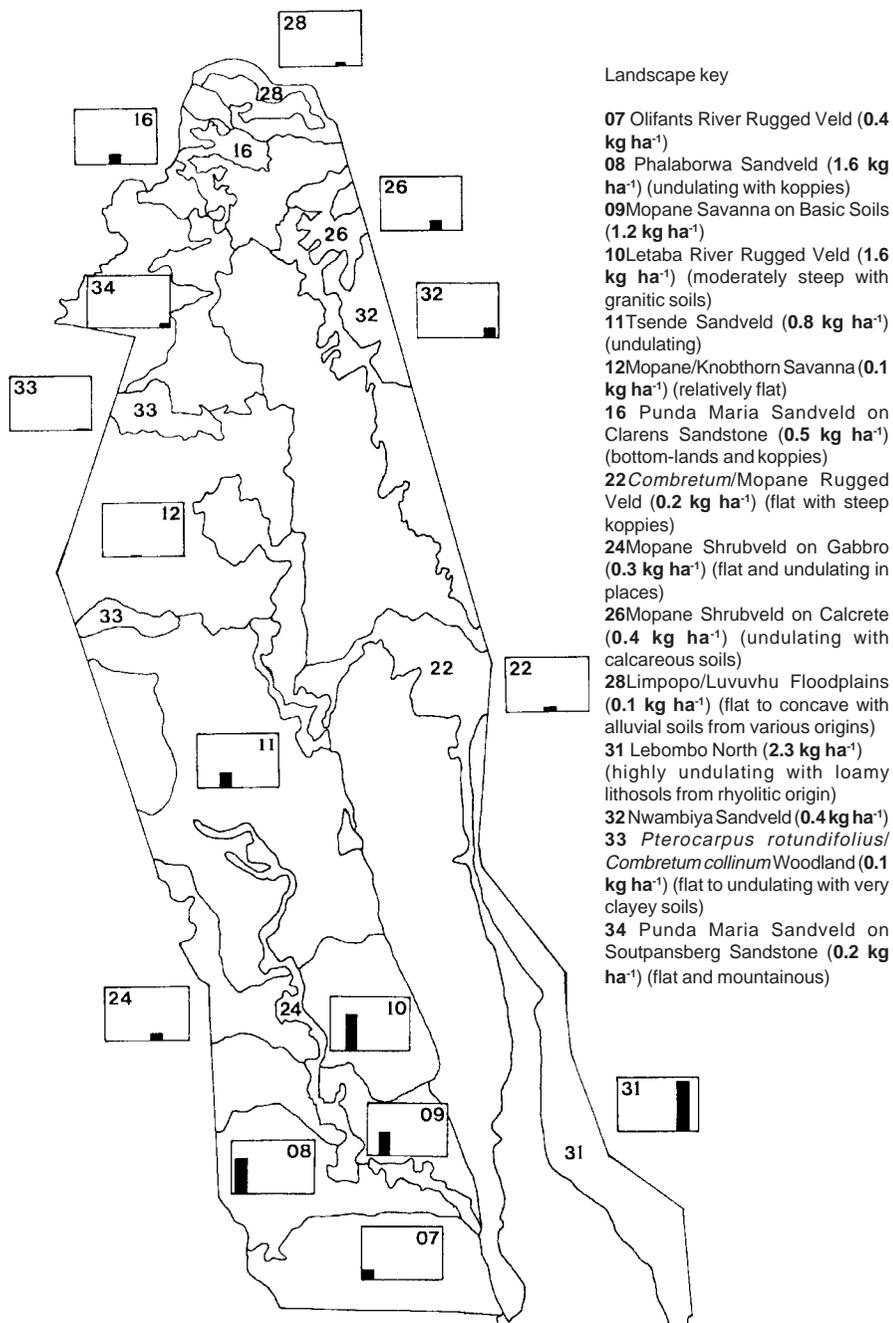


Fig. 1. Total live colony biomass (excl. reproductives) of *Macrotermes natalensis* (Hav.) estimated for different landscapes in the northern Kruger National Park. (Landscapes and environmental factors which most strongly affect termite biomass are disclosed – Gertenbach, 1983.)

Table 4. Comparison of dry/wet body mass ratios between the different castes and subcastes by means of general linear modelling of the least-squares means (LSMs), where differences were very highly significant*** ($P < 0.001$), highly significant** ($P < 0.01$), significant* ($P < 0.05$) or not significant (NS). [Prob > |t|; H_0 : $LSM_i = LSM_j$]

Comparison of ratios	Significance level
Workers vs. Major soldiers	NS
Workers vs. Minor soldiers	***
Workers vs. Nymphs	**
Workers vs. Queen	NS
Workers vs. King	***
Major soldiers vs. Minor soldiers	***
Major soldiers vs. Nymphs	NS
Major soldiers vs. Queen	NS
Major soldiers vs. King	***
Minor soldiers vs. Nymphs	***
Minor soldiers vs. Queen	***
Minor soldiers vs. King	NS
Nymphs vs. Queen	NS
Nymphs vs. King	***
Queen vs. King	***

known what effect there is of land characteristics on biomass of large colonies, as no significant difference was found between habitat types. It is possible that such an effect was masked by bootstrapping, in that caste investment in different landscapes was not investigated per se, but projected through extrapolation of data (Table 3).

Landscape 31 (Lebombo North) being a highly undulating mountain range, and having high rainfall and loamy soils, supports high biomass per mound (Fig. 1, Table 5a, Appendix 1a). Landscapes 26 (*Colophospermum mopane* Shrubveld on Calcrete) and 33 (*Pterocarpus rotundifolius/Combretum collinum* Woodland), though, are low in termite biomass. The topography of the latter two landscapes is undulating to flat; they have low rainfall and very clayey, calcareous soils.

Weathering of granite and rhyolite in landscapes 10 (Letaba River Rugged Veld) and 31 has given rise to well-drained sandy and loamy soils (Gertenbach 1983; Meyer *et al.* 1999; Venter, unpubl.). In these areas total biomass is high (Fig. 1, Table 5b, Appendix 1b). In contrast, alluvial soils made up of various river deposits are present in landscape 28, where termite biomass is low.

It appears that *M. natalensis* is high in biomass on medium elevated land (250–400 m) within the elevation range of the northern KNP, and low in biomass in areas of lower elevation (200–250 m) or higher elevation (400–450 m) (Appendix 1a,b).

Table 5. Comparisons (A vs. B) of live biomass per mound class (a) and total biomass (b) between different landscapes, where conservative (P_c : probt, $v = 9$) or liberal (P_l : probnorm, $v = \infty$) probabilities were highly significant** ($P < 0.01$), significant* ($P < 0.05$) or not significant ($P > 0.05$). (Only landscapes where termites occur (biomass > 0) were compared, and only comparisons where at least P_l was significant are shown.)

Landscape A		Landscape B		t	P_c	P_l
a						
Biomass in Small mounds of Landscape 8	Biomass in Small mounds of Landscape 26	Biomass in Small mounds of Landscape 26	Biomass in Small mounds of Landscape 26	1.97116	NS	*
Biomass in Small mounds of Landscape 26	Biomass in Small mounds of Landscape 26	Biomass in Small mounds of Landscape 28	Biomass in Small mounds of Landscape 28	-2.08993	NS	*
Biomass in Small mounds of Landscape 31	-2.63384	*	**			
Biomass in Medium mounds of Landscape 9	Biomass in Medium mounds of Landscape 9	Biomass in Small mounds of Landscape 33	Biomass in Small mounds of Landscape 33	2.08934	NS	*
Biomass in Medium mounds of Landscape 11	Biomass in Medium mounds of Landscape 11	Biomass in Medium mounds of Landscape 33	Biomass in Medium mounds of Landscape 33	2.05582	NS	*
Biomass in Medium mounds of Landscape 28	Biomass in Medium mounds of Landscape 28	Biomass in Medium mounds of Landscape 31	Biomass in Medium mounds of Landscape 31	1.99608	NS	*
Biomass in Medium mounds of Landscape 31	-2.01884	NS	*			
		Biomass in Medium mounds of Landscape 33	Biomass in Medium mounds of Landscape 33	3.09717	*	**
b						
Total biomass in Landscape 10	Total biomass in Landscape 10	Total biomass in Landscape 12	Total biomass in Landscape 12	1.99459	NS	*
Total biomass in Landscape 10	Total biomass in Landscape 10	Total biomass in Landscape 28	Total biomass in Landscape 28	2.43089	*	*
Total biomass in Landscape 12	Total biomass in Landscape 12	Total biomass in Landscape 31	Total biomass in Landscape 31	-2.11814	NS	*
Total biomass in Landscape 28	Total biomass in Landscape 28	Total biomass in Landscape 31	Total biomass in Landscape 31	-2.60841	*	**

Biomass in Land Types

The K12 (Klipkoppies) land type has low mountains and hills with a high local relief and annual rainfall. This land type sustains high *M. natalensis* biomass of medium mounds (Table 6a, Appendix 2a). Low termite biomass occurs in the Nw1 (Nwambiya), Ph8 (Tsende) and Ph12 (Dothole) land types; they are plateau-like plains with low local relief and rainfall.

Additionally, a perspective on soil color is gained by the examination of land type effects on total biomass of the species surveyed. Grey rather than red soils seem to be preferred by these termites (Table 6b, Appendix 2b).

Areas of high local relief (81 m) have high termite biomass but low biomass where the relief is low (6–14 m) (Appendix 2a,b).

Overall Biomass

Higher *M. natalensis* biomass occurs on lithosolic soils (often loamy) than on calcareous clay (Table 5, Appendix 1). Neocutanic soils (e.g., Oakleaf form) of the Pa5 land type (resembling landscape 26) consist of

Table 6. Comparisons (A vs. B) of live biomass per mound class (a) and total biomass (b) between different land types, where conservative (P_c : probt, $v = 9$) or liberal (P_l : probnorm, $v = \infty$) probabilities were very highly significant*** ($P < 0.001$), highly significant** ($P < 0.01$), significant* ($P < 0.05$), marginally significant ($P \approx 0.05$) or not significant ($P > 0.05$). (Only land types where termites occur (biomass > 0) were compared, and only comparisons where at least P_l was significant are shown.)

Land type A	Land type B	t	P_c	P_l
a				
Biomass in Medium mounds of the K12 Land Type	Biomass in Medium mounds of the Nw1 Land Type	2.20953	MS	*
Biomass in Medium mounds of the K12 Land Type	Biomass in Medium mounds of the Pa5 Land Type	2.04319	NS	*
Biomass in Medium mounds of the K12 Land Type	Biomass in Medium mounds of the Ph5 Land Type	2.04796	NS	*
Biomass in Medium mounds of the K12 Land Type	Biomass in Medium mounds of the Ph8 Land Type	6.17475	***	***
Biomass in Medium mounds of the K12 Land Type	Biomass in Medium mounds of the Ph10 Land Type	1.97119	NS	*
Biomass in Medium mounds of the K12 Land Type	Biomass in Medium mounds of the Ph12 Land Type	2.83426	*	**
Biomass in Medium mounds of the Pa3 Land Type	Biomass in Medium mounds of the Ph8 Land Type	2.50334	*	*
Biomass in Medium mounds of the Ph4 Land Type	Biomass in Medium mounds of the Ph8 Land Type	3.60657	**	***
Biomass in Medium mounds of the Ph6 Land Type	Biomass in Medium mounds of the Ph8 Land Type	4.79669	***	***
Biomass in Medium mounds of the Ph6 Land Type	Biomass in Medium mounds of the Ph12 Land Type	2.13046	NS	*
Biomass in Medium mounds of the Ph7 Land Type	Biomass in Medium mounds of the Ph8 Land Type	4.65196	**	***
Biomass in Medium mounds of the Ph7 Land Type	Biomass in Medium mounds of the Ph12 Land Type	2.13420	NS	*
b				
Total biomass in the K12 Land Type	Total biomass in the Le5 Land Type	2.00063	NS	*
Total biomass in the K12 Land Type	Total biomass in the Pa5 Land Type	2.18550	MS	*
Total biomass in the K12 Land Type	Total biomass in the Ph6 Land Type	2.19817	MS	*

loosely aggregated soil particles (Soil Classification Working Group 1988, 1991), and supports low termite biomass (Tables 5a, 6b). This soil form also features in landscapes 28 and 35 (Gertenbach 1983), where low or zero termite biomass occurs (Fig. 1, Table 5). The moderately deep, red, structured clay (often calcareous) of the Ph12 land type (resembling landscape 33) is classified under the Shortlands form (Venter 1990). It is therefore inferred that this species frequently occurs in low biomass on Oakleaf and Shortlands soil forms. In contrast, this principal species can be expected in high biomass on Mispah, Glenrosa and Hutton forms, which comprise the soil layers of landscape 10 (resembling the southern part of Ph7 land type) (Gertenbach 1983; Venter 1990). No vegetation correlations were found. It is shown that higher rainfall zones ($650\text{--}700\text{ mm a}^{-1}$) are preferred by the species under study to areas receiving lower rainfall ($225\text{--}525\text{ mm a}^{-1}$) (Appendices 1, 2).

It was calculated that the average live biomass (incl. nymphs but excl. reproductives) per square unit area of *M. natalensis* across the entire northern KNP, based on a priori units, is approximately 0.51 kg ha^{-1} (51 kg km^{-2}). Average dry biomass is calculated as 0.11 kg ha^{-1} (11 kg km^{-2}). This means that more than 500 metric tons (500 000 kg) of live termite tissue (ca. 110 t dry) of this dominant species occurs across the study area. This figure could be raised above 600 t if foraging neuters (workers and soldiers) outside mounds are anticipated to occur (Darlington 1982, 1991; Meyer *et al.* 2000).

DISCUSSION

Although workers outnumber other castes (Meyer *et al.* 2000), their biomass (Table 2) is second to that of the massive major soldiers because of reduced body mass (Table 1). This means that while workers are numerically more abundant, they make a smaller contribution to colony biomass than the major soldiers (Table 2). There is thus a considerable cost of defence (Oster & Wilson 1978), as more biomass gets diverted into the soldiers than into workers. However, turnover of the workers is faster than for soldiers because of seemingly greater soldier longevity (Bouillon 1970; Darlington 1991). Young workers are directly involved with new biomass acquisition, as they feed the nymphs (Badertscher *et al.* 1983). Older workers are responsible for other duties such as foraging further from the colony centre, and may therefore be subjected to greater predatory losses. However, as colonies get larger there is a reduction in defence cost, because soldier proportions decrease with colony size (Meyer *et al.* 2000).

Live biomass (neuters only) of small and medium epigeal *M. natalensis*

colonies amounts to 0.167 kg and 1.374 kg (Table 2), and compares favorably to that of *M. bellicosus* (0.177 and 0.846 kg, respectively – derived from Collins 1981b). Dry biomass of neuters (steriles) in large mounds of *M. michaelseni* in Kenya (Darlington 1991) is higher (5.330 kg) than that of *M. natalensis* in the KNP (0.905 kg), due to larger body size and mass.

From both a landscape and land type perspective on termite biomass, it is clear that *M. natalensis* occurs more profusely in areas of undulation rather than where the land morphology (topography) is flat or concave (Tables 5, 6, Appendices 1, 2). In like manner it has been shown that mound density is high where drainage is sufficient and low where it is poor (Meyer *et al.* 1999). In Australia, Holt & Easey (1993) found higher mound-building termite biomass on yellow soils than on red soils. The present study suggests that grey soils are dominated in certain areas. Coloration is due to different iron oxides decreasing in quantity, as wetness increases, from red to yellow to grey (Venter, pers. comm.). Grey soils are usually leached and sandy.

High relief, which augmented *M. natalensis* biomass in the area surveyed, is due to more valleys and hills (undulation). Increased runoff from slopes favors the termites (Meyer *et al.* 1999). Yet another explanation may be that the vegetation is affected and, in turn, termite biomass, although no clear preferences could be shown. Eggleton *et al.* (1994, 1996) suggested that termites are not critically limited by the presence or absence of particular tree species in an assemblage.

High rainfall zones of the study area are shown to be preferred by *M. natalensis* (Appendices 1, 2). A similar relationship between mound density and rainfall was previously shown (Meyer 1997). Pomeroy (1978) predicted a lower limit of 300 mm a⁻¹ for *Macrotermes subhyalinus* (Rambur) in Uganda. In the northern KNP, rainfall generally increases from north to south (Gertenbach 1980; Dent *et al.* 1987; Venter 1990). Collins (1977) found a positive correlation between rainfall and litter production in West Africa and, in the present study, it is probable that more litter occurs southerly than northerly. This likelihood is further supported by the fact that elephants occur in higher population densities in this southern region (Olifants–Phalaborwa–Shangoni–Shingwedzi block), and more branches are brought down from the tree canopy and added to the litter pool. These factors are likely to influence termite biomass.

Constant grazing and reduction of fire intensity increase tree and shrub biomass. Because *M. natalensis* consumes woody litter (e.g., Ferrar 1982b), an increase in woody vegetation will be beneficial. Woody biomass may decrease on sandy, granitic soils in areas with a moderate

to low rainfall (Venter 1990). It was shown in the present study that termite biomass is proliferated on granitic soils, but reduced where rainfall is lower. Higher biomass of woody plants in high rainfall areas may therefore be responsible for increased termite biomass in those areas.

If for purposes of comparison the live biomass of *M. natalensis* (0.51 kg ha^{-1}) is related to that of the whole genus (1.4 kg ha^{-1} – Meyer, unpubl.), this represents 36% of macrotermitine biomass (excl. *Odontotermes* Holmgren) in the northern KNP. The present study showed that live average neuter biomass, estimated at 0.50 kg ha^{-1} , is much lower than that of *M. bellicosus* (4.7 kg ha^{-1}) in Nigeria (Collins 1981a) and *M. subhyalinus* (6.0 kg ha^{-1}) in Senegal (Lepage 1974). As biomass is density-dependent, a lower result per unit area (by an order of magnitude) for the northern KNP is obtained, compared to that of the Afrotropical region in the northern hemisphere. It is not always clear, though, whether the biomass figures given by Collins (1981a) and Lepage (1974) relate to weighted or non-weighted density according to the proportion of areas. In the case of the latter, results can be misleading in that they are overestimates and a poor reflection of abundance and hence biomass per unit area (Meyer *et al.* 1999; Holt, pers. comm.). It is also possible that higher termite biomass is propagated through higher net primary productivity in equatorial habitats (tropics) leading to higher rates of litter production than in more arid (mesic) areas at higher latitudes, where metabolic costs of living are increased, such as in the sub-tropical KNP.

As termites are generally soil-dwelling ectotherms, they are reliant upon properties of the soil solum (habitat). The Macrotermitinae are less dependent on these factors because of mound architecture and fungal symbiosis (e.g., Lee & Wood 1971; Fraser 1993). Termites are also able to patchily change soil properties in the environment (Pomeroy 1976, 1978).

We showed that a number of interrelated environmental factors influence termite biomass. Although a degree of heterogeneity occurs within landscapes (Gertenbach 1983), principal soil and vegetation patterns have been recognized (e.g., Meyer 1997). Major parameters such as geology, terrain morphology and woody vegetation are reflected in land types (Venter 1990), with emphasis on soil. The land is shaped by forces best described by local relief, slope class (land unit), and stream frequency. The underlying factor determining termite biomass thus seems to be drainage (Meyer *et al.* 1999; Grant, pers. comm.).

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Appendix 1. Landscape attributes where significant differences were shown for live mound-based biomass (a) and total biomass (b) of *Macrotermes natalensis* (Hav.) in the northern Kruger National Park. (Landscape classification from Gertenbach, 1983; rainfall estimates from Dent *et al.*, 1987.)

High termite biomass		Low termite biomass	
Landscape	Attributes	Landscape	Attributes
a			
<small>SMALL</small>			
Landscape 31	Highly undulating (mountain range) Lithosolic soils ca. 650 mm annual rainfall	Landscape 26	Undulating Calcareous soils (high in lime) ca. 350 mm annual rainfall
<small>MEDIUM</small>			
Landscape 31	Highly undulating 300–400 m elevation Loamy soils ca. 650 mm annual rainfall	Landscape 33	Flat to undulating 400–450 m elevation Very clayey soils ca. 450 mm annual rainfall
b			
Landscape 10	Moderately steep slopes 250–400 m elevation Granitic soils ca. 475 mm annual rainfall	Landscape 28	Flat to concave (koppies absent) 200–250 m elevation Alluvial soils (various origins) ca. 225 mm annual rainfall
Landscape 31	Highly undulating 300–400 m elevation Lithosols from rhyolitic origin ca. 650 mm annual rainfall	Landscape 28	Flat to concave 200–250 m elevation Alluvial soils from various origins ca. 225 mm annual rainfall

Appendix 2. Land type attributes where significant differences were shown for live mound-based biomass (a) and total biomass (b) of *Macrotermes natalensis* (Hav.) in the northern Kruger National Park. (Land type classification from Venter, 1990; rainfall estimates from Dent et al., 1987.)

High termite biomass		Low termite biomass	
Land type	Attributes	Land type	Attributes
a			
MEDIUM			
K12 land type	Low mountains and hills High to moderately undulating 81 m local relief ca. 700 mm annual rainfall	Nw1, Ph8 & Ph12 land types	Plains (plateau-like) Flat to slightly undulating 9–14 m local relief 400–525 mm annual rainfall
Pa3, Ph4, Ph6 & Ph7 land types	[No clear correlations between land types of high termite biomass]	Ph8 land type	–
b			
K12 land type	High to moderately undulating mountains and hills 81 m local relief Grey to brown soils ca. 700 mm annual rainfall	Pa5 & Ph6 land types	Concave to slightly undulating plains 6–12 m local relief Red to brown soils 225–475 mm annual rainfall

