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Research article

Intracolonial demography of the mound-building termite *Macrotermes natalensis* (Haviland) (Isoptera, Termitidae) in the northern Kruger National Park, South Africa

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Summary. This paper reports on the number of individuals in *Macrotermes natalensis* (Hav.) colonies of different sized mounds in the northern Kruger National Park. Mounds were fully excavated, termites collected by means of vacuuming, and colony size estimated by sub-sampling. The proportion of termites in the mound (above and underground sections) amounts to more than 70% of the colony; the rest being present in the surrounding soil (excavated beyond mound perimeter). It was estimated that, on average, small mounds contain more than 5000, medium mounds more than 45 000, and large mounds more than 200 000 individual termites. A highly significant relationship between total individuals (N) and mound height (h) was found, given by $\ln N = 7.893 + 1.093\,h$ ($r = 0.92$). Highly significant correlations ($r_S > 0.90$) were found between and within caste numbers, and their respective ratios given. The proportion of soldiers was found to change as colonies grew larger.

Key words: Termite colonies, caste composition, Termitidae, *Macrotermes natalensis*, Kruger National Park.

Introduction

Termites are pivotal in nutrient cycling and hence an important ecosystem component that requires analysis (e.g., Pomeroy, 1978; Lamotte and Bourlière, 1983; Nkunika, 1986; Meyer et al., 1999). The rationale for carrying out this research is dichotomously described: intracolonially and ecologically. The former implies trophallaxis – exchange of nutrients between individuals on contact (La Fage and Nutting, 1978), either stomodeally (mouth-to-mouth) or proctodeally (from the rectum). Secondly, termites have been shown to fix nitrogen (Curtis and Waller, 1998). If the nitrogen fixation rate per individual termite is known, caste numbers and proportions provided by the present study can be used to accurately derive overall nitrogen fixation, as rates of fixation vary among species and castes via microbes and fungi (e.g., Matsumoto and Abe, 1979; Collins, 1983). Furthermore, termites are important in the capture and release of essential ions and soil nutrients and in the degradation of complex carbohydrates (cellulose) to simple carbon compounds. When plants, in turn, take up these compounds, the available nitrogen facilitates growth (Hesse, 1955). Nitrogen fixation is necessary, as mobile nitrogen is easily leached from the root zone into deeper soil horizons (Tainton, 1988).

In order to understand the influence of termites in natural ecosystems it is necessary to estimate the biomass and food consumption of colonies. It is therefore vital to obtain baseline data and other fundamental information about this species, so that the necessary projections can be made. It is anticipated that biomass and food consumption will be researched using the results and insights gained from this study, so as to improve upon the management plan of this large game sanctuary (Braack et al., 1997).

The distribution and density of termite mounds in the northern Kruger National Park (KNP) was determined for *Macrotermes* Holmgren (Meyer et al., 1999). *Macrotermes natalensis* (Haviland) was shown to be the most abundant (dominant) species in the northern KNP and therefore the best candidate for further analysis. Determining the number of individuals and caste composition of *M. natalensis* colonies of different sizes is the principal focus of this study, as caste composition is essential to estimate the effects of termites on ecosystem processes.

Darlington (1984) estimated the populations of termite mounds in Kenya using methyl bromide fumigation. In the present study, new methods of mound excavation (circular trench-digging), termite collection (vacuuming) and sub-sampling were used. Previously, perpendicular trench-digging (e.g., Darlington, 1984) was undertaken and another sub-sampling method used (e.g., Maldague, 1964; Collins, 1981). The sub-sampling technique (Clark et al., 1971; Clark and Turton, 1973) we used for termites is one that has been used for anthelmintics and should give reliable estimates of population size (Wood et al., 1995).

The information from the census of the mounds is used to analyze the extent to which caste proportions differ between mounds of different sizes. Interrelationships of castes and subcastes are analyzed to assess changes in caste composition during colony development.

Materials and methods

Study area

The northern KNP comprises approximately 981 000 ha (ca. 52%) of the total area of the park, and is located between the Olifants (24°02′30″S) and Limpopo Rivers (22°19′21″S) (Meyer et al., 1999). This area has mainly mopane vegetation, with a mean annual rainfall of approximately 500 mm and an elevation of roughly 375 m above sea level (Acocks, 1988; Coates Palgrave, 1988; Dent et al., 1987). Seasonal variability in the context of the region is low, due to insignificant spatial differences in temperature and humidity (Meyer, 1997).

Determination of the volume of mounds

The volumes of the mounds were calculated from the measurement of height (soil surface to mound apex) and diameter (radius is from mound centre to perimeter). Since the shapes of the mounds were complex, the volumes were estimated from the formulae for solids of different shapes.

Assuming mounds have a circular base, the surface volume of mounds was determined via integral calculus by means of 360° rotation of areas about an axis in order to generate solids defined across a range of curvature. The volume formulae of the solids so produced were rendered precision by different denominators according to particular mound shapes. Mounds B, C and E were paraboloids of revolution ($\pi/2\, r^2h$), A and F conventional cones ($\pi/3\, r^2h$), and D and 5 concavely tapered ($\pi/7\, r^2h$), where r is radius and h perpendicular height. Subterranean volume was considered cylindrical (πr^2h), because it pertains to depth (subterranean height) and diameter as excavated (beyond mound perimeter).

Excavation of mounds and termite collection

Three small (height: 0.30–1.34 m), two medium (1.35–2.59 m), and two large (2.60–5.00 m) mounds of *M. natalensis* were fully excavated. Alate release in the KNP predominantly occurs during December and February (Meyer, pers. obs.), although alate production is not the main focus of this study. Darlington (1986) has found that seasonality plays an insignificant role in the production of sterile castes.

Excavations were done in the Phalaborwa and Woodlands regions during daylight hours when no dispersal or foraging was evident. A circular trench (as deep as termites occurred, often a metre down) was dug beyond the mound perimeter so as to include the pediment. This took 1–3 days depending on mound size. Excavation was performed by gradually exposing sections of the mound, while digging proceeded towards the centre. It was observed that workers continually closed the holes made by pick strokes, thereby preventing ant predation.

Termites were carefully sought and collected by means of a large, industrial vacuum cleaner powered by a 3.5 kVA generator. Vacuuming was applied, as too much soil would otherwise have been removed had all the mound soil been collected. This is due to the relative largeness of the *M. natalensis* mounds in the study area. Termites were vacuumed by inserting the vacuum pipe directly into mound cavities (shafts). Other individuals were swept off broken mound fragments by a gentle stroke of the rubber nozzle. Small fragments were unavoidably collected too. Termites that found themselves on fungus comb or loose soil were sucked up together with the substrate, the soft comb crushing to smaller pieces upon entering the pipe. Remaining individuals and nymphs were handpicked with forceps. Roughly 60% of the termites were vacuumed and 40% hand-extracted. The breeding pair was not removed until all individuals had been collected in order to reduce disturbance among the uncollected colony members. No emigration occurred during excavations and the same applied after sunset (confirmed by night observation). It is however possible that underground foragers returning to the nest during daytime (*sensu* Lepage, 1981; Darlington, 1982) may have been excluded by the ring-trench, especially for the smaller mounds.

Separation from soil and debris

Vacuum samples that consisted of termites mixed with soil were placed in water so that the termites could be separated by flotation (Collins, 1981). Ninety-litre stackable dustbins were used to facilitate ease of transport to various, distant camps. The soil-and-water mixture was frequently stirred with a spade or hose-pipe connected to a running tap. Floating individuals were skimmed off using sieves, whereas sunken individuals were collected by pouring the fluid through stackable sieves with apertures ranging from 500–3350 μm. Clean sand and gravel remained, while suspended clay and silt were removed with the fluid. Termites were handpicked (forceps) from between fungus comb pieces and other debris, and then preserved in methanol for a short period of time.

Sampling and counting processes

Estimation of colony sizes was done using a helminthological method (Clark et al., 1971; Clark and Turton, 1973). The total volume of fluid for a particular mound (5–30 l depending on colony size) was vigorously transferred between two buckets until an even distribution of termites was obtained throughout the fluid. While this transfer was taking place, a sample of 200–500 ml of fluid was taken from beneath and within the stream of fluid, moving the sample bottle from side to side. This process was repeated eight times for each of the medium and large mounds, and by so doing eight equal samples per mound were obtained.

Populations of small mounds were counted in full.

Only termite heads were counted, as they were frequently found detached from the abdomens. This was presumably due to the vacuuming and fluid transfer processes. Because sterile nymphs were handpicked, they were easily recognized. The degree of pigmentation was indicative of the difference between workers (brown) and nymphs (white), and soldiers (red-brown for majors; orange-brown for minors) and nymphs (white). Because of intermediate sizes in workers (e.g., Sands 1998), they were not subdivided. However, it is estimated that approximately 30% of the worker caste is made up of the smallest individuals (minors).

Statistical procedures

Data processing and analysis were conducted using SAS (SAS Institute, 1989 a, b). In order to normalize the data, counts were transformed using the natural logarithm (Steel and Torrie, 1980). Variation around the mean was determined by making use of the two-tailed t distribution

Table 1. Nest populations of *Macrotermes natalensis* (Hav.) showing abundance in different castes and developmental stages of the colony, i.e. small, medium and large mound sizes. (Back-transformed extrapolated counts are geometric means and variation given by lower and upper confidence limits (α (2) = 0.05; v = 7). Whole populations were counted for small mounds and thus no statistical variation exists. The percentage of a caste or group that it comprises in the total population is given in parentheses)

MND	Size	Total individuals			Workers			Major soldiers			Minor soldiers			All soldiers		
		Lower	Mean	Upper	Lower	Mean (%)	Upper	Lower	Mean (%)	Upper	Lower	Mean (%)	Upper	Lower	Mean (%)	Upper
C	s	–	4 173	–	–	2 704 (64.8)	–	–	870 (20.8)	–	–	574 (13.8)	–	–	1 444 (34.6)	–
D	s	–	5 051	–	–	2 645 (52.4)	–	–	1 798 (35.6)	–	–	566 (11.2)	–	–	2 364 (46.8)	–
E	s	–	7 926	–	–	4 086 (51.6)	–	–	2 277 (28.7)	–	–	677 (8.5)	–	–	2 954 (37.3)	–
A	m	41 191	46 048	51 476	20 373	22 905 (49.7)	25 752	9 447	10 740 (23.3)	12 210	5 908	6 782 (14.7)	7 785	15 400	17 530 (38.1)	19 954
B	m	42 610	45 621	48 846	16 881	18 029 (39.5)	19 256	16 784	18 005 (39.5)	19 315	3 776	4 268 (9.4)	4 825	20 591	22 281 (48.8)	24 111
F	l	104 439	107 526	110 704	63 556	66 407 (61.8)	69 385	18 673	21 064 (19.6)	23 761	7 005	8 031 (7.5)	9 207	26 079	29 154 (27.1)	32 592
5	l	289 845	301 905	314 467	181 611	188 714 (62.5)	196 095	36 437	39 948 (13.2)	43 798	14 389	16 349 (5.4)	18 577	51 585	56 394 (18.7)	61 652

MND	Size	Sterile nymphs			Alates (adults & nymphs, resp.)			Abiotic parameters						
		Lower	Mean (%)	Upper	Lower	Mean (%)	Upper	Excavation date	Mound height (m)	Mound diameter (m)	Excavated depth (m)	Excavated diameter (m)	Mound volume (m^3)	Subterranean volume (m^3)
C	s	–	25 (0.6)	–	–	–	–	Mar. 1998	0.73	1.05	0.90	1.68	0.32	2.00
D	s	–	42 (0.8)	–	–	–	–	Mar. 1998	1.20	1.00	0.65	1.60	0.13	1.31
E	s	–	886 (11.2)	–	–	–	–	Mar. 1998	1.25	1.10	0.50	2.00	0.59	1.57
A	m	4 776	5 523 (12.0)	6 387	–	–	–	Feb. 1998	2.00	1.10	0.95	1.76	0.63	2.31
B	m	4 805	5 240 (11.5)	5 715	36	55 (0.1)	83	Feb. 1998	1.60	1.85	0.35	3.55	2.15	3.46
F	l	10 995	11 691 (10.9)	12 430	–	–	–	Apr. 1998	3.80	2.60	0.85	4.00	6.73	10.68
5	l	49 340	53 863 (17.8)	58 800	2 059	2 476 (0.8)	2 979	Oct. 1995	4.30	4.30	1.00	4.80	8.92	18.10

and the standard error of the mean (SE). As back-transformation was carried out, values are reported geometrically.

Multiple regression models of natural log-transformed caste numbers against mound dimensions and volumes were run. Mound parameters were not transformed, because their transformation does not affect the distribution of *Y* nor any least-squares consequences. As criterion to include the best set of variables in the model, the C_P statistic of Mallows was employed, which is similar to the predicted error sum of squares.

General linear modelling (GLM) was carried out on log-transformed caste numbers and on square-root transformed proportions as percentages of the total population. GLM was performed by making use of the least-squares means pre-classified into three levels of mound size: small, medium and large. Differences in caste numbers or proportions between different mound sizes were verified for significance by the *t* test. No post hoc assumptions that pro tem sequence is indicative of cause and effect were made.

Results

The main conclusion of Darlington (1984) was that if a nest is not fumigated before excavation, net emigration from the nest occurs. The effect of our ring-trenching technique may be equivalent to fumigation in that it isolates the population, especially that of smaller nests. It must be reiterated that emigration from nests was not evident in our study, nor was the return of workers or soldiers from foraging passages.

Population estimates are presented in Table 1. A higher percentage of the total population of medium-sized mounds (32%) was counted (sub-sampled) than for large mounds (14%). However, comparing the various percentage standard deviations (%SDs), no apparent increase in accuracy was obtained for medium mounds. Low to relatively low %SDs were achieved on average for the individuals in total (2.1%), the workers (2.9%), the major and minor soldiers (4.3%; 7.0%), and the worker and soldier nymphs (5.9%).

The total number of individuals ± SD occurring in small mounds is 5717 ± 1963 ($n = 3$), in medium mounds 45835 ± 302 ($n = 2$), and in large mounds 204716 ± 137447 ($n = 2$) (Table 1). The number of termites extrapolated to occur in the different castes gives an accurate indication of their abundance in the respective colonies, as relatively little variation occurs around the means.

Numbers of individuals were positively related to mound dimensions. Height provided the best predictor of population size (Table 2a). Mound diameter and excavated depth were not significant. For example, if the height of a mound (5.3 m) encountered in the Limpopo-Luvuvhu valley is used (Meyer, 1997), then the population (total individuals) is estimated to be approximately 880000. Mound volume (m^3) was found to be a significant parameter in estimating population size (Table 2b). Workers increase at a faster rate (steeper regression slope) than the other castes (except nymphs) as mounds become larger (Table 1). Subterranean termitarium volume was not significantly correlated with nest population sizes (Table 2b).

A reason why mound volume ($0.91 > R > 0.76$) was slightly poorer related to caste numbers than mound height ($0.95 > R > 0.83$) could be because of the assumption that mounds have circular bases. For the volume of conical mounds having ellipsoidal bases, the formula $V = 1.808\, r_1 r_2 h$ can be used (Janse van Rensburg, pers. comm.). In the case of the other mound shapes, future improvement is recommended.

Comparing caste numbers between the various colonies, no significant differences for major and minor soldiers and worker and soldier nymphs were found between medium and large mounds (Table 3a). As for proportions (percentages of the total population), only the soldiers differed significantly between medium and large mounds as well as between large and small mounds (Table 3b; Fig. 1a).

Discussion

Mound-building termites in the KNP were never found to establish nests that were deeper than 1 m below ground level, as soils (esp. northwards) are relatively shallow (Venter, 1986). It is possible that the populations of the mounds were underestimated, even though the subterranean and immediate

Table 2a. Relationship between numbers of individuals in each caste and mound dimensions using a multiple regression procedure with maximum R^2 improvement. Mound height, mound diameter, excavated depth and excavated diameter (m) were the abiotic variables considered in the analysis. (Disclosed models were significant ($P < 0.05$) to highly significant ($P < 0.01$). Two, three and four-variable models were not significant)

Caste	Model	R^2	C_P	F	Prob > F	Abiotic variable	Intercept estimate	Slope estimate (indep. varb.)
Total individuals	1-variable (indep.)	84.5%	– 0.3737	27.3	0.0034	Height	7.8930	1.0927
Workers	1-variable (indep.)	89.8%	– 0.3788	44.0	0.0012	Height	7.1763	1.1394
Major soldiers	1-variable (indep.)	74.1%	0.0038	14.3	0.0129	Excavated diameter	6.1636	0.9530
Minor soldiers	1-variable (indep.)	74.7%	– 0.5313	14.7	0.0121	Height	5.9656	0.8954
All soldiers	1-variable (indep.)	73.2%	– 0.1492	13.7	0.0140	Height	7.2520	0.8920
Sterile nymphs	1-variable (indep.)	69.2%	– 0.2937	11.3	0.0202	Height	3.6020	1.7454

Table 2b. Relationship between numbers of individuals in each caste and mound volume using a multiple regression procedure with maximum R^2 improvement. Mound volume and subterranean volume (m^3) were the abiotic variables considered in the analysis. (Disclosed models were significant ($P < 0.05$) to highly significant ($P < 0.01$). Two-variable models were not significant)

Caste	Model	R^2	C_P	F	Prob > F	Abiotic variable	Intercept estimate	Slope estimate (indep. varb.)
Total individuals	1-variable (indep.)	76.0%	1.0502	15.8	0.0105	Mound volume	9.1006	0.4009
Workers	1-variable (indep.)	81.9%	1.0083	22.6	0.0051	Mound volume	8.4271	0.4210
Major soldiers	1-variable (indep.)	62.9%	1.3415	8.5	0.0334	Mound volume	7.9002	0.3247
Minor soldiers	1-variable (indep.)	62.2%	1.0296	8.2	0.0351	Mound volume	6.9894	0.3162
All soldiers	1-variable (indep.)	63.1%	1.2202	8.6	0.0329	Mound volume	8.2571	0.3203
Sterile nymphs	1-variable (indep.)	58.4%	1.1867	7.0	0.0455	Mound volume	5.5870	0.6201

Table 3a. Comparison of termite numbers of the various castes and subcastes (majors and minors) between different developmental colony stages, based on *pro forma* mound size (S – small; M – medium; L – large), by means of general linear modelling. (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: $\mathrm{LSMean}_i = \mathrm{LSMean}_j$)

Comparison between mounds	Total individuals	Workers	Major soldiers	Minor soldiers	All soldiers	Sterile nymphs
S_i vs. M_j	**	**	**	**	**	*
M_i vs. L_j	*	*	NS	NS	NS	NS
L_i vs. S_j	***	***	**	***	***	*

Table 3b. Comparison of termite proportions (percentage data) of the various castes and subcastes (majors and minors) between different developmental colony stages, based on *pro forma* mound size (S – small; M – medium; L – large), by means of general linear modelling. (Differences were significant* ($P < 0.05$) or not significant (NS); Prob > | t |, H_0: $\mathrm{LSMean}_i = \mathrm{LSMean}_j$)

Comparison between mounds	Workers	Major soldiers	Minor soldiers	All soldiers	Sterile nymphs
S_i vs. M_j	NS	NS	NS	NS	NS
M_i vs. L_j	NS [1]	NS	NS	*	NS
L_i vs. S_j	NS	NS	NS	*	NS

[1] Marginally significant ($P = 0.0507$).

surrounding sections of the mound were excavated. Darlington (1982) found that subterranean foraging passages could comprise a considerable area around a mound. This fraction of the colony's population (in the foraging zone) might have been excluded from our samples.

The construction of the bulk of a nest above soil surface in the form of a mound may be related to thermoregulatory requirements (e.g., Fraser, 1993; Korb and Linsenmair, 1998 a, b, 1999; Turner, 2000). The fact that aboveground volume can be used to estimate the population of mounds (Table 2 b) indicates that there is a close relationship between the size of a colony's population and its construction activities.

Mound and colony size

A mature mound of *Macrotermes michaelseni* (Sjöstedt) in Kenya was estimated to contain 1.3 million neuters (total population excl. nymphs) (Darlington, 1991), while *Macrotermes bellicosus* (Smeathman) mounds in Nigeria sheltered approximately 360000 neuters (derived from Collins, 1981). For mounds of *Macrotermes ukuzii* Fuller in Swaziland and *Macrotermes carbonarius* (Hagen) in Malaysia roughly 48000 and 30000 neuters, respectively, were calculated to occur (derived from Rohrmann, 1977 and Matsumoto, 1976 as given by Darlington, 1984). Darlington (1984) is of the opinion that the numbers given for *M. ukuzii* and *M. carbo-*

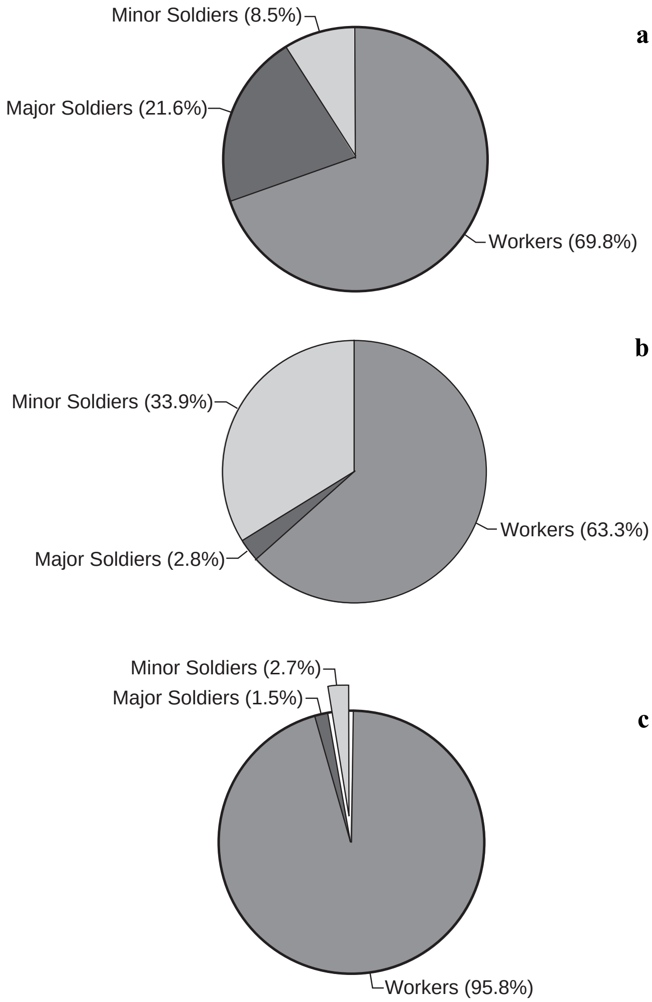

Figure 1. Caste composition of nest populations (excl. foraging zone) of *Macrotermes natalensis* (**a**) (pres. stud.), *M. ukuzii* (**b**) (Rohrmann, 1977) and *M. michaelseni* (**c**) (Darlington, 1991) as percentages of adults

narius are underestimates. The colony sizes given for *M. ukuzii* are quite reasonable considering their relatively small pinnacle mounds (Meyer, 1997). Using the example of the mound in the Limpopo-Luvuvhu valley, we estimate that it has a neuter (sterile) population of ca. 480000 termites (total individuals minus all nymphs). Mound size is however not always clearly stated by the authors cited, but suffice to say that across species a mature *Macrotermes* mound could contain 440000 neuters.

Predictions and implications

In order to predict the number of major soldiers in a mound by using aboveground measurements (i.e. height), the number of all soldiers minus that of minor soldiers could be utilized in the regression equations (Table 2a). In this way mound height can be used instead of excavated diameter, as the latter is a man-defined dimension albeit is where termites occurred. The indication of excavated diameter as significant in the regression model could thus be considered a Type I error, as this relationship is difficult to explain biologically. Judging from the volume regressions presented in Table 2b, mound volume appears to have the best explanatory power.

Twice as many workers occur as soldiers (2:1). Soldiers have a protective duty mainly in the sense of accompanying workers on foraging excursions and barricading holes to prevent intruders from entering the mound (e.g., Lepage, 1981; Darlington, 1982, 1991; Jmhasly and Leuthold, 1999a, b). Workers older than thirty days engage in foraging (Badertscher et al., 1983). The ratio of workers to minor soldiers is 8:1 (Fig. 1a). Polyethism (division of labour) between major and minor soldiers occurs in macrotermitine species, especially those foraging in the open like *Macrotermes vitrialatus* (Sjöstedt) (Coaton and Sheasby, 1972; Badertscher et al., 1983). Major soldiers pose a formidable threat to predators such as ants because of increased body size. Collins (1981) found a ratio of 2:1 for minor and major soldiers, which is the opposite of that found in the present study (1:3). Colonies of *M. natalensis* have thus fewer minor soldiers than major soldiers, while the opposite is the case for *M. bellicosus*. *Macrotermes ukuzii* and *M. michaelseni* also have more minor soldiers than major soldiers (Fig. 1b, c).

Numbers of individuals increase with mound size as shown by the positive relationships (Table 2). The proportion of soldiers in the colony decreases between the intermediate (ergonomic) and advanced (reproductive) colony stages (Table 3b). We conclude that the proportions of the other castes stay constant between different developmental stages.

The ergonomic stage is a transitional period of colony growth during which non-reproductive individuals are added to the colony (Oster and Wilson, 1978). In the present study this is the case for all castes (Table 1), although the proportion of soldiers actually decreases from small and medium to large mounds (Table 3b). This was also found for *M. michaelseni* in Kenya (Darlington and Dransfield, 1987). The declining proportion of soldiers in colonies as they increase in size may be related to reduced surface area to volume ratios as mounds get larger. This means that by less exposure in surface area to sun and predators the microclimate is kept at an optimal level (thermoregulation) and the mounds are easier to defend. Disinvestment in soldiers benefits the colony in that worker proportions and hence nutrient cycling (*sensu* Curtis and Waller, 1998) is increased, as more labour is required for food gathering beyond denuded areas often seen around large nests. A continual trade-off between workers and soldiers (within neuters) is thus sustained.

The composition of *M. natalensis* colonies that has been determined in this study can be used to quantify food conversion into biomass vis-à-vis the different castes. Furthermore, the data presented here could serve future purpose insofar as the regional influence of this species on nutrient cycling is concerned.

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