Intracolonial demography, biomass and food consumption of *Macrotermes natalensis* (Haviland) (Isoptera: Termitidae) colonies in the northern Kruger National Park, South Africa

by

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AIM LOW, BORING; AIM HIGH, SOARING – Charles R. Swindoll

In Tribute to my Father

This thesis is dedicated to my father, GERT HENDRIK WILHELM MEYER (Vic), for his continuous support and encouragement. He was often the only one who said that I must not throw in the towel.

I will be forever grateful for the many camping and hiking trips he exposed me to. I also thank him for his great love of the outdoors and keen interest in nature from which I developed my interest in biology.

You have to *work a little harder* than the next one
Be a little smarter if you want to survive
You have to *move a little faster* than the last time

Know just what you're after and never look behind
You have to look out for number one
Set your sights on the stars and the Son
Look out for Number One
You have to push a little harder, push a little harder, yes!

Fly just like an arrow don't you ever lose sight
Walk the straight and narrow every day and every night
You have to look out for Number One...

Inspired by the original motion picture soundtrack *Staying Alive* (Paramount Pictures)
'Look Out for Number One' by Tommy Faragher (B. Stephen Foster/T. Marolda)
Stigwood International Publ. Inc./Famous Music Corporation (P) 1983 RSO Records, Inc.

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SUMMARY

Thesis title:	Intracolonial demography, biomass and food consumption of *Macrotermes natalensis* (Haviland) (Isoptera: Termitidae) colonies in the northern Kruger National Park, South Africa
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This thesis reports on the number of individuals in *Macrotermes natalensis* (Hav.) colonies, their biomass and food consumption in the northern Kruger National Park (KNP).

The ecology of *M. natalensis* is largely undocumented despite the abundance of colonies in southern African savannas. New approaches to mound excavation, sub-sampling and data management are introduced. Via the intracolonial demography of colonies the contribution of each caste in number or proportion is determined. Using this information in combination with body mass and mound density data, biomass per unit area has been computed indicating the importance of this termite in synecology. The measurement of food consumption gives further insight as to how much litter is removed, fragmented and redistributed as nutrients in the ecosystem.

Mounds were completely excavated, termites collected by means of vacuuming, and colony size estimated by sub-sampling. It was estimated that, on average, small mounds contain more than 5 000, medium mounds more than 45 000, and large mounds more than 200 000 individual termites. A highly significant relationship between total number of individuals (N) and mound height (h) was found, given by $\ln N = 7.893 + 1.093h$ ($r = 0.92$). The proportion of soldiers was found to change as colonies grew larger.

In order to derive biomass estimates, a statistical bootstrap procedure was carried out using three databases: body mass, colony population sizes and mound density. Live biomass for small, medium and large mounds was found to be 0.17, 1.40 and 4.16 kg. 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 was calculated to be 0.51 kg/ha (0.051 g/m^2) and 0.11 kg/ha (0.011 g/m^2). 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 undulating 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.

Major workers fetch woody litter outside the nest through ingestion into the section of the crop and gizzard. Gut contents were dried, weighed, ashed and reweighed. The ash mainly represents soil particles. The ash-free mass of food that is consumed during a single foraging trip by a foraging individual is 0.166 ± 0.009 mg (CI). Frequency of foraging trips between the mound and food source was observed using translucent tubing. The annual food consumption is given by the formula $365mnp/t$, where m = individual mass of ashed crop-gizzard contents, n = number of foraging major workers, p = daily foraging period, and t = individual time spent between nest and food source. Food consumption of this termite in the northern KNP is calculated to be 20.2 kg/ha/yr.

It is shown that termites are primary decomposers and contribute to litter fragmentation and the recycling of nutrients into the soil. This thesis gives greater insight into aspects such as colony development, biomass investment and resource utilization of *M. natalensis* in the northern KNP.

OPSOMMING

Tesis-titel:	Intrakoloniale demografie, biomassa en voedselverbruik van *Macrotermes natalensis* (Haviland) (Isoptera: Termitidae) kolonies in die noordelike Nasionale Krugerwildtuin, Suid-Afrika
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Graad:	Ph.D.

Hierdie tesis raporteer oor die aantal individue in *Macrotermes natalensis* (Hav.) kolonies, hul biomassa en voedselverbruik in die noordelike Nasionale Krugerwildtuin (NKW).

Die ekologie van *M. natalensis* is grootliks ongedokumenteer ten spyte van die volopheid van kolonies in savannes van suidelike Afrika. Nuwe benaderings tot hoop-opgrawing, sub-monsterneming en data-beheer word aangevoer. Deur die intrakoloniale demografie van kolonies word die bydra van elke kaste bepaal in aantal of proporsie. Gebruikmakende van hierdie inligting in kombinasie met liggaamsmassa en hoopdigtheidsdata, is biomassa per eenheidsoppervlak bereken in aanduiding van die belangrikheid van hierdie termiet in synekologie. Die mate van voedselverbruik gee verdere insig oor hoeveel afval verwyder, gefragmenteer en herversprei is as voedingstowwe in die ekostelsel.

Hope was heeltemaal opgegrawe, termiete versamel deur middel van stofsuig, en kolonie-grootte beraam deur sub-monsterneming. Dit was per gemiddeld beraam dat klein hope meer as 5 000, medium hope meer as 45 000, en groot hope meer as 200 000 individuele termiete bevat. 'n Hoogsbeduidende verwantskap tussen totale aantal individue (N) en hoophoogte (h) was verkry, gegee deur $\ln N = 7.893 + 1.093h$ ($r = 0.92$). Dit was bevind dat die proporsie van soldate verander sooswat kolonies groter raak.

Om biomassa-syfers af te lei, was 'n statistiese 'bootstrap'-prosedure gevolg gebruikmakende van drie databasisse: liggaamsmassa, kolonie-bevolkingsgroottes en hoopdigtheid. Dit was bevind dat lewende biomassa vir klein, medium en groot hope 0.17, 1.40 en 4.16 kg is. Droë/nat liggaamsmassa-verhoudings was vir werkers (23.7 %), groot soldate (20.3 %), klein soldate (35.3 %), nimfe (17.1 %), koning (35.4 %) en koningin (20.8 %) vasgestel. Gemiddelde lewende en droë biomassa was bereken as 0.51 kg/ha (0.051 g/m^2) en 0.11 kg/ha (0.011 g/m^2). Geologie, geomorfologie, elevasie, lokale reliëf, grondpatrone en jaarlikse reënval was die invloedrykste abiotiese faktore in die bepaling van termiet-biomassa, hetsy direk of indirek. Termiet-biomassa is hoog in golwende areas waar die elevasie 250–400 m is, waar granitiese en riolitiese gronde voorkom, en waar jaarlikse reënval hoog is (650–700 mm) in die konteks van die gebied.

Groot werkers gaan haal hout-afval buite die nes deur ingestie in die gedeelte van die krop en maag. Die ingewandsinhoud was gedroog, geweeg, veras en herweeg. Die as verteenwoordig hoofsaaklik gronddeeltjies. Die asvrye massa van voedsel wat verbruik is gedurende 'n enkele voedselsoektog deur 'n soekende individu is 0.166 ± 0.009 mg (BI). Frekwensie van voedselsoektogte tussen die hoop en voedselbron was geobserveer deur gebruik te maak van deursigtige buise. Die jaarlikse voedselverbruik word gegee deur die formule $365mnp/t$, waar m = individuele massa van veraste krop-maaginhoud, n = aantal voedselsoekende groot werkers, p = daaglikse voedselsoekende periode, en t = individuele tyd spandeer tussen nes en voedselbron. Voedselverbruik van hierdie termiet in die noordelike NKW word bereken op 20.2 kg/ha/jr.

Dit was bevind dat termiete primêre afbrekers is en 'n bydra lewer tot die fragmentasie van afval en hersirkulasie van voedingstowwe in die grond. Hierdie tesis gee groter insig in aspekte soos kolonie-ontwikkeling, biomassa-belegging en hulpbronbenutting van *M. natalensis* in die noordelike NKW.

CONTENTS

Chapter 1

INTRODUCTION

The richest termite fauna occurs in Africa (Skaife *et al.* 1979). African Macrotermitinae construct the largest, most complex structures of all invertebrates (Collins 1981; Fraser 1993). Mounds of *Macrotermes* are widely distributed throughout the Afrotropical region on various kinds of soil (*e.g.* Hesse 1955). The Macrotermitinae are fungus-growing termites (Petch 1906) and comprise one of four subfamilies of Termitidae. *Macrotermes* is represented by 12 Afrotropical species of which 6 are southern African (Ruelle 1978). Social behaviour of termites favours large colony size because of improved defence, improved homeostasis (thermoregulation), and improved division of labour as polyethism (division in tasks) and cooperation becoming more highly evolved (Wilson 1972).

Systematics and classification of termites

Eusocial societies, such as those of termites, are usually typified by division of labour (reproductive suppression of subordinates by dominant breeders), overlap of generations, and cooperative care of the brood (Sherman *et al.* 1995; Shellman-Reeve 1997). Termites differ from hymenopterous social insects (ants, bees, wasps) in that they are hemimetabolous, their castes bisexual and they do not have known subsocial groups. Termites are structurally most closely related to cockroaches (Blattodea) (Josens 1983). Recently, it is postulated that the Isoptera is nested within the Blattaria and, above them, the Dictyoptera (mantids, cockroaches) (Eggleton 2001).

Termites of the family Termitidae differ from other termites by having 4-jointed tarsi, usually a fontanelle and ocelli and small anterior wing stumps. The soldier and worker castes have a narrow, saddle-shaped pronotum with an anteriorly-raised median lobe (Hill 1942; Skaife *et al.* 1979).

The Termitidae is the largest family, comprising about 80 % of isopteran species (Ruelle 1989).

Termite surveys

South African termites have been well surveyed taxonomically, due to the National Survey of Isoptera (1955–1982) conducted by W.G.H. Coaton and J.L. Sheasby (Plant Protection Research Institute). In the Kruger National Park (KNP), 22 genera of termites are known to occur. The mound-building genera in the KNP are *Macrotermes* Holmgren (Termitidae: Macrotermitinae), *Cubitermes* Wasmann (Termitidae: Termitinae), *Amitermes* Silvestri (Termitidae: Termitinae), *Odontotermes* Holmgren (Termitidae: Macrotermitinae) and *Trinervitermes* Holmgren (Termitidae: Nasutermitinae) (Coaton 1962). Of the two genera of large fungus-growers (*Macrotermes* and *Odontotermes*) in South Africa, *Macrotermes* is well studied (Ruelle 1989). *Macrotermes subhyalinus* (Rambur) and *Macrotermes bellicosus* (Smeathman) are probably the two species best studied in Africa (Ruelle *et al.* 1975). *Macrotermes natalensis* (Haviland), which is the most abundant in the northern KNP (Meyer *et al.* 1999), is regrettably less studied.

Global, continental and regional distribution

Emerson, as quoted by Light (1946a), postulated that the world distribution of termites has northern and southern limits roughly coinciding with the mean annual isotherm of 10°C. Thus, globally they occur mainly between 45°N and S latitudes, other than on high altitudes where it is too cold or in deserts where food is unavailable (Harris 1969).

Many termites are found in arid regions where temperatures are high and rainfall is low. It has been suggested that such termites must burrow deep in order to reach water far underground. However, they may obtain much of the water they need from their moist food and compensating feeding habits (Skaife *et al.* 1979).

In southern Africa, *Macrotermes* is naturally distributed north of a rough line formed by the Great Kei and Orange Rivers. Colonies per unit area increase in a northerly direction (Coaton 1949).

Basic termite biology

Caste differentiation can only be detected when nymphs have completed about two thirds of their development (Skaife *et al.* 1979). Neuters (workers and soldiers) are usually blind and wingless and they are sterile (Harris 1969; Lee & Wood 1971).

Workers are the sole builders of the nest and mound. Their first priority is to carry out repairs in order to keep the colony sealed-off from possible invasion by predators and the elements. Only adult workers gather food. They remove and transport eggs from the breeding female (queen) to the nursery and care for them (Skaife *et al.* 1979), as well as the resultant hatchlings. Workers also feed and groom the queen (Light 1946b) and feed the soldiers (Grassé 1949). In species of Macrotermitinae, they are also responsible for the cultivation and weeding of fungi (Petch 1906).

Soldiers are responsible for the defence of the colony. They accompany the foraging workers, patrol galleries and attack any intruders. According to Light (1946b) and Marais (1975), they also guard the queen. In *Macrotermes*, soldiers have formidable mandibles.

Reproductive alates become the founders of new colonies after they have shed their wings and successfully burrowed. According to Collins (1981), only 0.5 % survive the onslaught of predatory animals.

The sole purpose of the small, primary male or king (no enlargement of the abdomen after casting of wings) is to fertilize the queen (Harris 1971; Lee & Wood 1971; Skaife *et al.* 1979). The primary queen of *M. natalensis* (after physogastry has taken place) is about 10 cm in length and unable to move from one locality to another.

Secondary reproductives are replacements of the initial primary pair (Fraser 1993). If the founding queen grows too old and her fertility wanes, the workers kill her by means of 'licking'. When she dies or is killed, the workers immediately set about giving a selected dozen of the alate nymphs 'special' food so that they are able to succeed her. Their sexual organs develop before the insects themselves are mature; they swell up and become secondary queens, slightly smaller than their predecessor (Skaife *et al.* 1979).

However, they are able to lay eggs much more rapidly than the primary queen, at least at first. If only one pair is developed, no others develop later in their presence. In some cases uneven numbers of kings and queens may develop at the same time (Kofoid 1946a; Marais 1975). There is evidence of aggression between queens in polygynous colonies (Brandl *et al.* 2001). The current trend of thinking is that pairs that develop from alate nymphs may be considered primary where recolonization or budding has taken place (Husseneder *et al.* 1999).

Tertiary reproductives are rare. They develop from specially fed and initially immature workers in the absence of a secondary queen and alate nymphs. Their fertility does not keep up with the colony's mortality rate and numbers dwindle until the population collapses. Tertiary females cannot lay eggs that will produce alates (Skaife *et al.* 1979).

The reproductives contribute to the distribution of the species by swarming or colonizing flights, choice of site of the new colony, excavation of the first galleries, and feeding and care of the first young (Krishna 1969).

Social behaviour

During the first stage of the life cycle, the king and queen produce nanitic (dwarfish) workers. Soldiers are produced only if there are enough workers, after which an increase in egg-production is prevalent. The second stage involves more egg-production by the adult pair (Fuller 1915).

After the nuptial flight the female settles on the ground. With the tip of the abdomen raised and wings fluttering, she gives off a scent (pheromone) to attract a male settling behind her. Both shed their wings. The male then follows the female as she looks for a suitable spot to burrow (Skaife *et al.* 1979; Braack 1991; Kaib 1999). Post-dealation, subterranean pairing is believed to take place tail-to-tail with heads in opposite directions. At first the pair rears nanitic workers, feeding them bodily secretions. During the first year, reproduction is slow and the colony consists of a few workers and the primary king and queen (Light 1946b; Skaife *et al.* 1979; Ruelle 1989; Braack 1991).

When extensive biparental investment occurs, both potential parents exhibit sexual selection (choosiness) through a repertoire of courtship behaviours: mate rejection, intra-sexual combat, intra-pair aggression, etc. (Shellman-Reeve 1999).

Mature colonies produce alates only during parts of the year (Collins 1981). Kalshoven (1930) showed that colonies under stress might rear alates earlier than usual. Because of increased burrowing habits in the other castes, cuticles have become weakly sclerotized, abdomens elongated, and body fluid susceptible to evaporation if individuals are exposed to prolonged, surface conditions (Kofoid 1946b).

Most species swarm early during the wet season, generally after a heavy downpour or a day later at sunset or at night (Ruelle 1979; Josens 1983). *Macrotermes* species are night-flying and produce eggs one week after swarming (Harris 1971). Some alates are physically kept back by workers to form a second or even third swarm later in the season (Skaife *et al.* 1979).

Soldiers are less active than workers unless stimulated by vibrations indicative of danger (Sands 1965a). Activity in the surface layers of the soil is strongly influenced by soil moisture and hence by temperature/rainfall combinations (Ferrar 1982a). During winter activities slow down; there is no breeding or egg-laying (abdomen of queen becomes slender) and little food gathering is evident (Skaife *et al.* 1979).

Allogrooming, a natural response when two termites meet, not only serves to remove dust, moulds and offending particles from each other, but also yields much desired secretions from gland cells (Kofoid 1946a). A continual exchange of nutrients exists within the society (trophallaxis) (Lee & Wood 1971).

Food and feeding behaviour

The natural diet of species of the Macrotermitinae is dead plant matter supplemented by cultivated fungi (Lee & Wood 1971). Some species of *Macrotermes* also utilize dry dung of herbivores as food (Nkunika 1986). Termites incidentally feed on lichens, algae, organic rich parts of nests, and skins of vertebrate corpses. Cannibalism and oophagy may occur (Wood 1978).

Grassé (1949) noted that the king and queen often consume eggs to supplement their diet. Workers may control proportions of various castes by cannibalism. They also consume unhealthy and wounded individuals and corpses. Protein conservation may occasionally contribute towards the survival of the colony. Workers give stomodeal food to the soldiers because they cannot feed themselves.

During foraging plant material is removed from the soil surface while foraging structures (sheeting) protect food and termites against the elements and predators (Fraser 1993). Workers of *M. natalensis* construct covered runways if they come out on the surface to feed or forage (Skaife *et al.* 1979).

Mound dynamics

Lee & Wood (1971) stated that the principal species in Africa constructing large mounds are *M. natalensis*, *Macrotermes falciger* (Gerstäcker), *M. subhyalinus* and *M. bellicosus*.

Mound-building behaviour

According to Howse (1970), *Macrotermes* workers begin building at random. When particles achieve a certain density on the ground, they become foci for building activity with the result that pillars are formed. When the pillars attain a certain height, they provide a new stimulus situation for the termites which then begin to build at right angles towards adjacent pillars, forming arches. Neighbouring arches are then joined so that a complete roof is constructed. The queen's presence stimulates construction. Building and enlarging of the mound are generally carried out after it has rained, when the surface of the mound is moist and soft (Skaife *et al.* 1979). However, *M. natalensis* builds all year round, as it largely uses clay from the moist subsoil (Bodot 1967).

Mound shape is determined by three forces: behaviour of particular species, nature of the soil, and climate (Harris 1971). Mounds of *M. natalensis* are conical. When the subsoil consists of clay or limestone, the mounds are very hard and difficult for

intruders to gain entry (Coaton & Sheasby 1972). When mounds become inactive, erosion acts faster on mounds (Lepage 1984).

Mounds of *M. natalensis* under 25 cm in height represent new colonies, whereas mature colonies may reach above 2 m (Fraser 1993). One of the highest mounds encountered during the present study was an isolated mound of 5.3 m tall in the Limpopo-Luvuvhu valley.

Importance of mounds to the termites

According to various sources, as reported by Fraser (1993), the purpose of a mound is to establish and maintain a microclimate suitable for termites, enable the species to penetrate environments that are otherwise hostile, allow the storage and cultivation of food, and allow build-up of large colonies.

In combination with the social behaviour of termites, termitaria tend to produce a condition of homeostasis by self-regulation of optimal conditions for development, maintenance and reproduction of the society (Emerson 1962). The air inside the nest is invariably humid and always contains a higher percentage of carbon dioxide than the atmosphere, due to the termites' respiration (Skaife *et al.* 1979). Bakshi (1962) reported that in the case of Macrotermitinae, humidity and temperature (microclimate) are regulated by the fungus garden. The maintenance of high humidity is an essential requirement for the survival of most species of termites (Lee & Wood 1971). Nest temperature inside mounds remains relatively constant because of mound architecture, although fluctuating with ambient temperatures (Korb & Linsenmair 2000).

Soil utilization and modification

Pomeroy (1976) found that *Macrotermes* mounds are composed of subsoil (from a depth of approximately 0.5–1.0 m), except those in valleys that consist of topsoil. According to Hesse (1955), some termite mounds are more fertile than the surrounding soil, because the subsoil is more fertile than the topsoil. Similarly, when the subsoil is less fertile than the topsoil, then termite mounds in turn are less fertile.

Termites possess a remarkably efficient means of reducing complex organic matter to simple ions (Pomeroy 1978). They cycle nutrients by taking organic matter underground and depositing excavated soil on the surface (Nutting *et al.* 1987).

Influences of termites on ecosystems

According to Marais (1989), the presence of termites may bring about an increase in ground cover density, plant height, organic material, organic carbon, mineral salts and pH towards mound centres as well as a deep, stone-free topsoil. Rooting capabilities of trees are enhanced. Herbivores tend to utilize the vegetation on these termitaria, due to improved palatability brought about by the higher nitrogen levels. According to Hesse (1955), increased plant growth is related to better drainage and improved structure of mound soil.

Consumption of dead plant matter in natural systems is not as noticeable during years of elevated rainfall, but in periods of drought, or if areas are brought under cultivation, the absence of dead material compels termites to feed upon live plants (Naude 1934; Coaton 1953). In the case of severe drought, live plant material will have been depleted by large herbivorous animals, and they will turn to dead plant matter (stubble) if still present. In such events, competition for food between the two animal groups may become extreme. However, mild droughts usually favour the termites, due to more dead plant matter becoming available to them. In general, they should be regarded as highly beneficial insects of undisturbed habitat.

Rationale behind termite research in the KNP

The ecology of *M. natalensis* is largely undocumented despite the abundance of colonies in southern African savannas, of which the KNP makes up a pristine part of their known distribution (Coaton 1962; Ruelle *et al.* 1975; Meyer *et al.* 1999). This project was initiated to set up a databank of termite indicators showing ecological prevalence in certain areas. The outcome will be influential in conservation planning if trend-setting (regular monitoring) is considered by the Scientific Services section of the KNP. The inclusion of termites as a functional group in the management plan is necessary, particularly for the northern KNP, because of the abundance and

conspicuousness of termite mounds in the landscapes. New approaches to mound excavation, sub-sampling and data management will be introduced in the methodology so as to estimate the importance of termites in the study area. The purpose of this thesis is to present the intracolonial demography, biomass and food consumption of *M. natalensis* colonies in the KNP, north of the Olifants River (24.04ºS).

The reason for measuring the demography of colonies intracolonially is to determine the contribution of each caste in number or proportion to the colony (Chapter 2). Using this information in combination with data on body mass (Chapter 3) and mound density (*e.g.* Meyer *et al.* 1999), biomass per unit area can be computed to indicate the importance of this termite in synecology (comparative systems ecology). The measurement of food consumption (Chapter 4) will give further insight as to how much litter is removed, fragmented and redistributed as nutrients in the system.

Termites are important in nutrient cycling (Pomeroy 1978; Lamotte & Bourlière 1983; Nkunika 1986; Meyer *et al.* 1999), because they form a pivot upon which other components in the ecosystem depend. If the influence of termites, as indicated by biomass density, is ignored, then litter removal cannot be adequately understood and appreciated, especially where the frequency of fire (also a litter remover) is low or suppressed. These are important management considerations to be taken into account by conservationists of natural areas, such as the KNP. Quantitative analysis of the colonies of this species, having the highest mound density in the northern KNP, will provide improved understanding of termite influence in the ecosystem. This understanding will be obtained by comparing estimates of termite biomass and consumption of food with those of other ecosystem components. The incorporation of termites into a model ecosystem, as presented in the flow chart (Fig. 1), allows for recognition and better representation of termites in the nutrient cycle. The chart was generated using nitrogen fluxes through desert termites (Schaefer & Whitford 1981) in an ecosystem comprising standing crops (boxes) and transfers (arrows). The most important pivots in the KNP (Braack *et al.* 1997) are considered to be fire and elephant, with sinks of leaching (downwards) and predation (upwards) (Fig. 1).

Apart from litter fragmentation (cellulose decomposition) and carbon release (Holt 1987), the link formed between termites and soil (Fig. 1) denotes nitrogen fixation (Curtis & Waller 1998). Carbon and nitrogen levels affect most important ecosystem processes, because living things are made up of carbon atoms and nitrogen facilitates growth (*e.g.* Schlesinger 1997; Tateno & Chapin 1997). The most abundant gas in the atmosphere is nitrogen which is captured or fixed by bacteria in root tissues of certain pod-bearing plants. Fixation is also carried out by termites and notably by fungi that the Macrotermitinae cultivate (Collins 1983). Nitrogen is otherwise leached out (Tainton 1988) and lost from terrestrial to aquatic systems.
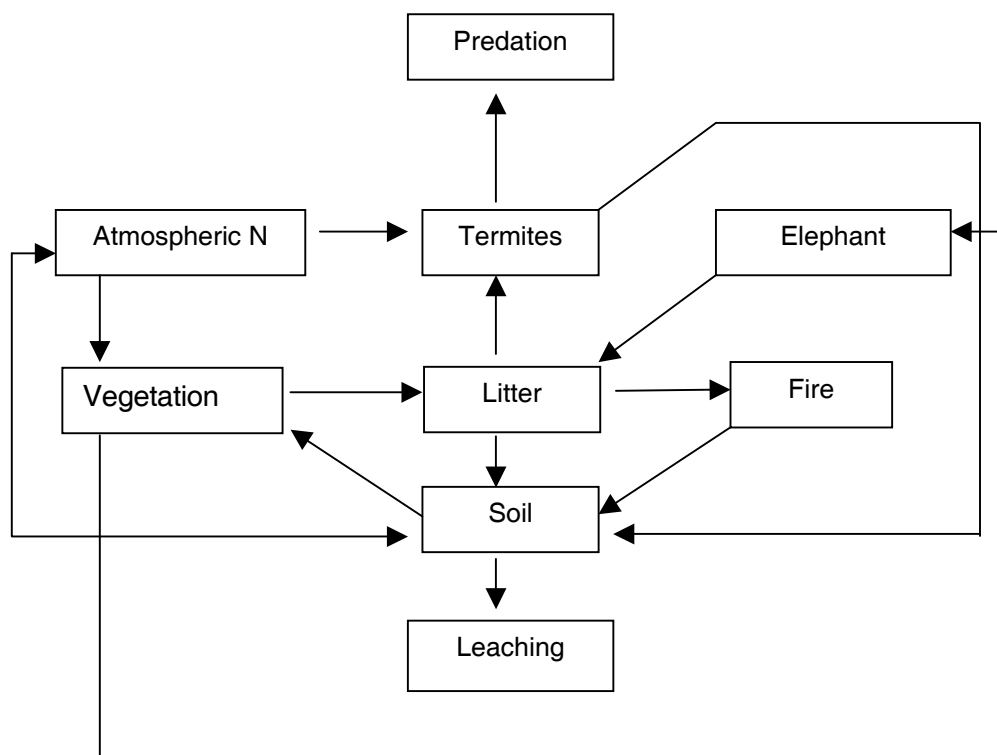
Fig. 1. Nutrient cycling scenario in Kruger National Park (Schaefer & Whitford 1981; Braack *et al.* 1997).

The distribution and density of *Macrotermes* populations were previously determined as part of a broader programme to monitor the influence of fire frequency, water distribution, and elephant density on biodiversity in the KNP (Braack *et al.* 1997; Meyer 1997; Meyer *et al.* 1999). It was found that approximately 1.1 million active termite mounds occur in the northern KNP, with an average density of 111 active mounds/km^2 (1.1/ha). The main mound-building genera were *Macrotermes*

(accounting for 62.4 % of all active mounds), *Cubitermes* (29.8 %), *Amitermes* (4.3 %), *Odontotermes* (2.1 %) and *Trinervitermes* (1.4 %). The dominant *Macrotermes* had a mound density of 0.73 active mounds/ha (73/km^2). *Macrotermes natalensis* and *M. ukuzii* Fuller were the dominant species with 0.27 and 0.25 mounds/ha, respectively. *Macrotermes* preferred sandy, granitic soils to basaltic soils. It was thought that the expanding and contracting effect of the basaltic soil (due to montmorillonitic clay) might influence the termites adversely, thus restricting their distribution and density in those areas. Basic information regarding the impact of experimental fire, artificial waterholes, and indirect stocking regimes on termites and other organisms is required in order to monitor changes in community structure (*e.g.* species richness and biomass).

Elephant impact in the KNP, especially in high density zones such as the area roughly occupied between the Olifants rest camp (24.01ºS) and the Mooiplaas ranger's post (23.51ºS) across the width of the park (31.08–31.89ºE), may affect termites. Elephants bring down branches from the tree canopy adding litter to the system (Fig. 1). Species of *Macrotermes* are responsible for fragmentation of the woody litter, and may also utilize dry dung of other herbivores as food (*e.g.* Nkunika 1986). Increased dung surrounding waterholes, due to the aggregation of herds, may patchily increase termite prevalence. Termite activity in turn improves the compacted soil by aeration (Sands 1965b). The important role that termites play as prime movers of organic content into foci (nest localities) should be recognized (Trapnell *et al.* 1976). Litter is also consumed by fire and brought down from the tree or shrub stratum (Fig. 1).

Traditionally, conservation policies focussed mainly on the mammal community because of its high visibility, tourism value, and the potential of some species to drastically alter local habitats. Establishment of data as basis for monitoring invertebrates was hitherto been poorly prioritized.

The intracolonial demography, biomass or consumption of any isopteran in the KNP has never been estimated before. The most apparent role of termites in savanna ecosystems is the consumption of litter (*e.g.* Josens 1983). As termites are important ecosystem components in the KNP (pivotal in nutrient cycling), it is vital to obtain baseline data on termites in order to effectively manage this natural asset.

Interrelationships between and within castes will be analyzed to assess colony development. Biomass is a good indicator of the amount of resources (carbon) that have been utilized in an ecosystem. When all these parameters are known, the influence of this pivotal species in the ecosystem can be established.

Chapter 2

Intracolonial demography of the mound-building termite *Macrotermes natalensis* (Haviland) (Isoptera, Termitidae) in the northern Kruger National Park, South Africa[2]

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 5 000, 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 $\ln N = 7.893 + 1.093h$ ($r = 0.92$). 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-

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[2] Meyer, V.W., R.M. Crewe, L.E.O. Braack, H.T. Groeneveld and M.J. van der Linde, 2000. *Insectes soc. 47*: 390–397.

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 given precision by different denominators according

to particular mound shapes. Mounds B, C and E were paraboloids of revolution ($\frac{\pi}{2}$ r^2h), A and F conventional cones ($\frac{\pi}{3}$ r^2h), and D and 5 concavely tapered ($\frac{\pi}{7}$ 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, 1989a,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 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 5 717 ± 1 963 ($n =$ 3), in medium mounds 45 835 ± 302 ($n = 2$), and in large mounds 204 716 ± 137 447 ($n = 2$) (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 880 000. 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.

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 ($\propto (2) = 0.05$; $v = 7$). 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 (m³)	Subterranean volume (m³)
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

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

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).

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: $LSMean_i = LSMean_j$)

| 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: $LSMean_i = LSMean_j$)

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).

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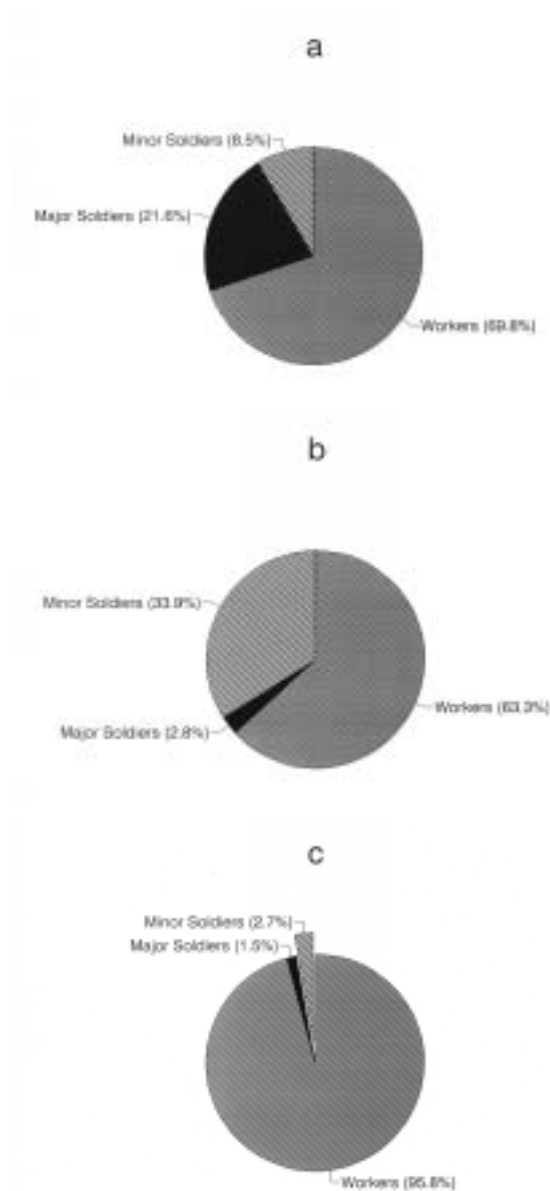
Figure 1. Caste composition of nest populations (excl. foraging zone) of *Macrotermes natalensis* (**a**) (pres. stud.), *M. ukuzii* (**b**) (Rohrmann, 1977) and *M. michaelseni* (**c**) (Darlington, 1991) as percentages of adults

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, 1998a,b, 1999; Turner, 2000). The fact that aboveground volume can be used to estimate the population of mounds (Table 2b) 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 360 000 neuters (derived from Collins, 1981). For mounds of *Macrotermes ukuzii* Fuller in Swaziland and *Macrotermes carbonarius* (Hagen) in Malaysia roughly 48 000 and 30 000 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. carbonarius* 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. 480 000 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 440 000 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.

Acknowledgements

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Chapter 3

Biomass of *Macrotermes natalensis* in the northern Kruger National Park, South Africa – the effects of land characteristics[3]

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 michaelseni* (Sjöstedt) and *Macrotermes falciger* (Gerstäcker) (Meyer *et al.* 1999). Collins (1981a) quantified biomass of *Macrotermes bellicosus* (Smeathman) populations in Nigeria. In Kenya, Darlington (1991) estimated biomass for colonies of *M.*

michaelseni. 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 under-appreciated. In future, re-surveying could be undertaken to assess trends in biomass oscillation and hence secondary production (turnover).

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.

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[3] Meyer, V.W., R.M. Crewe, L.E.O. Braack, H.T. Groeneveld & M.J. van der Linde. 2001. Sociobiology 38: 431–448.

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) were 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

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 (*n* = 10)	3.08 ± 0.36 (*n* = 9)	23.66 ± 2.92 (*n* = 9)
Major soldier	69.80 ± 2.27 (*n* = 10)	14.12 ± 1.15 (*n* = 9)	20.26 ± 2.92 (*n* = 9)
Minor soldier	17.18 ± 1.20 (*n* = 10)	6.13 ± 0.59 (*n* = 9)	35.27 ± 2.92 (*n* = 9)
Nymph	4.142 ± 0.736 (*n* = 8)	0.706 ± 0.112 (*n* = 7)	17.11 ± 3.52 (*n* = 7)
King	149.3 ± 234.4 (*n* = 2)	52.6 ± 50.2 (*n* = 2)	35.42 ± 34.15 (*n* = 2)
Queen	7044[1] ± 789 (*n* = 2)	1461[1] ± 2025 (*n* = 2)	20.76 ± 34.15 (*n* = 2)

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

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 (*n* = 300)	0.272 ± 0.027 (*n* = 300)	1.682 ± 0.394 (*n* = 300)
Major soldiers	0.115 ± 0.048 (*n* = 300)	1.006 ± 0.140 (*n* = 300)	2.135 ± 0.343 (*n* = 300)
Minor soldiers	0.010 ± 0.001 (*n* = 300)	0.096 ± 0.015 (*n* = 300)	0.211 ± 0.039 (*n* = 300)
Nymphs	0.001 ± 0.002 (*n* = 300)	0.022 ± 0.003 (*n* = 300)	0.135 ± 0.046 (*n* = 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:				$\overline{X}_i$	$\overline{X}_{ii}$	$\overline{X}_{iii}$	…	$\overline{X}_{ccc}$	
COLONY POPULATIONS (Meyer et al., 2000)		Small	3 obs. (whole populations)	SECOND	3 obs.	3 obs.	3 obs.	3 obs.	3 obs.	Number of individuals in small mounds
					1	2	3	…	300	
					$\overline{X}_i$	$\overline{X}_{ii}$	$\overline{X}_{iii}$	…	$\overline{X}_{ccc}$	
		Medium	16 obs. (eight aliquots per mound)		16 obs.	16 obs.	16 obs.	16 obs.	16 obs.	Number of individuals in medium mounds
					1	2	3	…	300	
					$\overline{X}_i$	$\overline{X}_{ii}$	$\overline{X}_{iii}$	…	$\overline{X}_{ccc}$	
		Large	16 obs. (eight aliquots per mound)		16 obs.	16 obs.	16 obs.	16 obs.	16 obs.	Number of individuals in large mounds
					1	2	3	…	300	
					$\overline{X}_i$	$\overline{X}_{ii}$	$\overline{X}_{iii}$	…	$\overline{X}_{ccc}$	
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	
					$\overline{X}_i$	$\overline{X}_{ii}$	$\overline{X}_{iii}$	…	$\overline{X}_{ccc}$	

Landscape key

07 Olifants River Rugged Veld (**0.4 kg ha^{-1}**)

08 Phalaborwa Sandveld (**1.6 kg ha^{-1}**)
(undulating with koppies)

09 Mopane Savanna on Basic Soils (**1.2 kg ha^{-1}**)

10 Letaba River Rugged Veld (**1.6 kg ha^{-1}**)
(moderately steep with granitic soils)

11 Tsende Sandveld (**0.8 kg ha^{-1}**)
(undulating)

12 Mopane/Knobthorn Savanna (**0.1 kg ha^{-1}**)
(relatively flat)

16 Punda Maria Sandveld on Clarens Sandstone (**0.5 kg ha^{-1}**)
(bottomlands and koppies)

22 *Combretum*/Mopane Rugged Veld (**0.2 kg ha^{-1}**)
(flat with steep koppies)

24 Mopane Shrubveld on Gabbro (**0.3 kg ha^{-1}**)
(flat and undulating in places)

26 Mopane Shrubveld on Calcrete (**0.4 kg ha^{-1}**)
(undulating with calcareous soils)

28 Limpopo/Luvuvhu Floodplains (**0.1 kg ha^{-1}**)
(flat to concave with alluvial soils from various origins)

31 Lebombo North (**2.3 kg ha^{-1}**)
(highly undulating with loamy lithosols from rhyolitic origin)

32 Nwambiya Sandveld (**0.4 kg ha^{-1}**)

33 *Pterocarpus rotundifolius*/*Combretum collinum* Woodland
(**0.1 kg ha^{-1}**) (flat to undulating with very clayey soils)

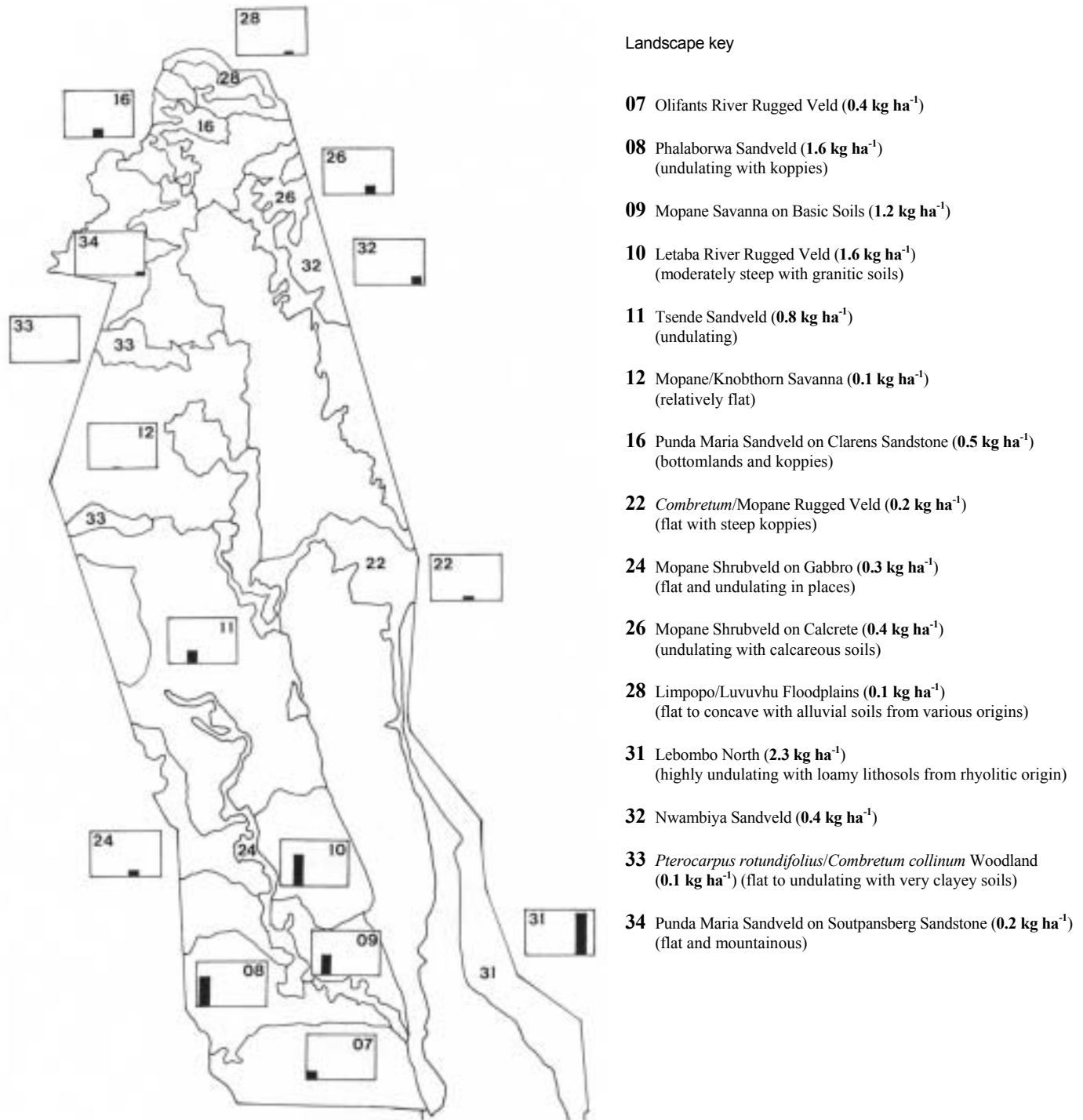**34** Punda Maria Sandveld on Soutpansberg Sandstone (**0.2 kg ha^{-1}**)
(flat and mountainous)

Fig. 1. Total live colony biomass (excl. reproductives) in kg ha^{-1} of *Macrotermes natalensis* (Hav.) estimated for different landscapes in the northern Kruger National Park. Data are given in the bar-charts overlaid on the map. (Landscapes and environmental factors which most strongly affect termite biomass are disclosed – Gertenbach, 1983.)

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) were 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.

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).

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$_j$]

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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	***

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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 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

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

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 Kl2 Land Type	Biomass in Medium mounds of the Nw1 Land Type	2.20953	MS	*
Biomass in Medium mounds of the Kl2 Land Type	Biomass in Medium mounds of the Pa5 Land Type	2.04319	NS	*
Biomass in Medium mounds of the Kl2 Land Type	Biomass in Medium mounds of the Ph5 Land Type	2.04796	NS	*
Biomass in Medium mounds of the Kl2 Land Type	Biomass in Medium mounds of the Ph8 Land Type	6.17475	***	***
Biomass in Medium mounds of the Kl2 Land Type	Biomass in Medium mounds of the Ph10 Land Type	1.97119	NS	*
Biomass in Medium mounds of the Kl2 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 Kl2 Land Type	Total biomass in the Le5 Land Type	2.00063	NS	*
Total biomass in the Kl2 Land Type	Total biomass in the Pa5 Land Type	2.18550	MS	*
Total biomass in the Kl2 Land Type	Total biomass in the Ph6 Land Type	2.19817	MS	*

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).

Biomass in Land Types

The Kl2 (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 colour 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 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 (650–700 mm a^{-1}) are preferred by the species under study to areas receiving lower rainfall (225–525 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 favourably 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 run-off from slopes favours 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 southwards than northwards. This likelihood is further supported by the fact that elephant 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			
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
MEDIUM			
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			
Kl2 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			
Kl2 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

Chapter 4

Food consumption and role of the fungus-growing termite *Macrotermes natalensis* in a South African savanna-woodland

Abstract. 1. This study quantifies and discusses food consumption by *Macrotermes natalensis* (Hav.) (Isoptera: Termitidae) based on gut analysis.

2. Gut contents were dried, weighed, ashed and reweighed. (The ash mainly represents soil particles in guts of older major workers.)

3. Frequency of foraging trips between the mound and food source was observed using translucent tubing.

4. The annual food consumption is given by the formula $365mnp/t$, where m = individual mass of ashed crop-gizzard contents, n = number of foraging major workers, p = daily foraging period, and t = individual time spent between nest and food source.

5. The ash-free mass of food that is consumed during a single foraging trip by a foraging individual is 0.166 ± 0.009 mg (CI).

6. Food consumption of this termite in the northern Kruger National Park is calculated to be on average 20.2 kg/ha/yr.

Key words. Food consumption, foraging, termite gut, Isoptera, Termitidae, Macrotermitinae, *Macrotermes*, *M. natalensis*, Kruger National Park, South Africa.

Introduction

Termite consumption of litter sometimes accounts for more than 30% of that which would otherwise have been subjected to radical mineralization by bush-fires (Collins, 1983; Josens, 1983; Holt, 1987; Martius, 1994; Abensperg-Traun & Milewski, 1995). The fungus-growing Macrotermitinae removed about 90–96% of the woody litter consumed by termites in Kenya and Nigeria (Buxton, 1981a; Collins, 1981a). The ecological importance of these termites in nutrient cycling is augmented by their high consumption per unit biomass, which is facilitated by nitrogen-rich fungal symbiosis

(Wood, 1978; Matsumoto & Abe, 1979; Collins, 1981b). The midgut (mesenteron) is a major centre of cellulose breakdown which is accomplished using enzymes that are acquired by the Macrotermitinae through ingestion of fungal nodules or synemata (mycophagy) rich in these enzymes (Sands, 1956; Martin & Martin, 1978). Mainly old major workers fetch forage (litter) outside the nest (e.g. Usher, 1975; Badertscher *et al.*, 1983). These adaptations allow fungus-growing termites to play a role in nutrient cycling that needs to be further quantified in order to gain an understanding of the way in which the system operates.

Macrotermes natalensis (Haviland) is found throughout southern Africa, with the exception of the western Cape (Ruelle *et al.*, 1975). In the northern wilderness areas of the Kruger National Park (KNP) this species is widespread and the most abundant termite (Meyer *et al.*, 1999).

Workers of *M. natalensis* venture outside the mound in underground passages exiting the soil surface near or at the food source, such as fallen branches or twigs. Evidence of foraging is left in the form of a thin sheet of soil constructed over the food source (e.g. Fraser, 1993). Sometimes the termites surface before they reach the litter and construct covered runways (Skaife *et al.*, 1979; Ferrar, 1982; Meyer, personal observation). Soldiers are fed by the workers and do not forage directly; protection that is offered to foraging workers is a cost of foraging (Lepage, 1981; Badertscher *et al.*, 1983; Darlington, 1991; Jmhasly & Leuthold, 1999a,b).

Food is ingested into the crop and gizzard of the foraging termite workers and transported back to the nest, where it is regurgitated for distribution and digestion (Wheeler, 1926; Noirot & Noirot-Timothée, 1969; Lepage, 1977; Sands, 1998). Stomodeal food in the foregut of foraging workers represents the amount of litter removed by their foraging effort. Transit of proctodeal food through the hindgut and faeces deposition (e.g. La Fage & Nutting, 1978; Badertscher *et al.*, 1983) is not the focus of this study.

This study was undertaken to quantify food consumption and to establish the role of this termite species in nutrient cycling (litter fragmentation). Because of the cryptic foraging behaviour of this species and response of retrieval displayed towards

disturbance, i.e. termites moving backwards and away from the point of interference (Coaton & Sheasby, 1972; Skaife *et al.*, 1979; Meyer, personal observation), estimation of removal of litter (mainly wood) is explored using analysis of gut contents rather than other methods that have been used.

Materials & Methods

Study area

In the northern KNP (South Africa), bordering on Mozambique in the east and Zimbabwe in the north, the landscape is dominated by mopane woodland (Acocks, 1988; Coates Palgrave, 1988). The mean annual rainfall is 494 mm (Dent *et al.*, 1987; Meyer *et al.*, 1999).

A foraging area (24.99745°S; 31.58453°E) for fine-scale study was chosen in close proximity to the laboratory, consisting of several foraging sites that belonged to ten colonies in the southern KNP. Data from the respective sites (where litter was actively consumed) was pooled for each colony. Classification of colonies based on small (height: 0.30–1.34 m), medium (1.35–2.59 m) and large (2.60–5.00 m) mound sizes was adopted from previous studies (Chapter 2).

Sampling and gut analysis

Foraging termites (major workers) were collected from beneath soil sheeting at natural food sources (woody litter) present at different distances around mounds. Woody litter was gently lifted and exit holes were immediately blocked to prevent fed foragers from departing and unfed foragers from arriving. Major workers were carefully picked up by the head and placed in Petri dishes using forceps (standard collection technique) – they numbered ca. 2 000 in total. It was not possible to collect termites without disturbance before foraging and afterwards, as the movement of foragers takes place underground (e.g. Coaton & Sheasby, 1972; Skaife *et al.*, 1979).

The major workers collected were promptly taken to the laboratory, where their gut contents were removed. This was done by applying pressure around the thorax and

abdomen, thereby forcing the contents through the anus. Care was taken not to remove the trophic membranes. The samples (gut contents) were dried over 48 hours at 70°C and weighed in the closed chamber of a microbalance to the nearest 0.0001 g. Individual mass of dry gut contents was obtained by dividing the mass of each of the ten samples by the number of individuals (ca. 200) represented in each sample. Dried samples were ashed in a bomb calorimeter or a muffle furnace (4 h at 600°C) and subsequently reweighed in order to determine the amount of organic material present in the gut. Both combustion and incineration gave similar ashing results. The ash mainly represents soil particles such as sand and quartz contained in the digestive tract of these workers.

In order to determine the fraction of gut contents present in the crop and gizzard, the digestive tracts of ten randomly selected foraging major workers were removed with forceps under a dissecting microscope. After the tract was uncoiled, the different sections were measured to the nearest 0.1 mm. The section of the crop and gizzard was considered a prolate ellipsoid (i.e. egg-shaped) and the formula $\frac{2}{3} \pi r^2 l$ used to determine its volume. The midgut, proctodeum and colon were cylindrical ($\pi r^2 l$) and the rectum was spherical ($\frac{4}{3} \pi r^3$).

Foraging frequency

The frequency of visits to the food source from the mound to the food and back was observed through a translucent Perspex tube (1 m x 40 mm) during different times of the day and night across seasons. The tube was laid horizontally as a passage directly between the mound and food source (e.g. Lepage, 1981) and covered with soil when observations were not being made. Observation was hampered by condensation inside the tube. Termites were reluctant to make use of tubes longer than a metre.

Determination of annual food consumption

The mass (percentage) of inorganic components (ash) found in the gut was subtracted from the dry mass of the gut contents. Since freshly foraged material (i.e. litter) is contained in the crop and gizzard, the proportion of gut contents in these regions

represents the amount of litter consumed. Foraging frequency was expressed as daily foraging period (time-span of foraging activity in 24 h day) divided by individual foraging time, i.e. number of return trips. The annual estimate of food consumed by this termite is thus given as $365mnp/t$, where m = individual ash-free mass of gut contents in crop-gizzard, n = number of foraging major workers, p = daily foraging period, and t = individual time spent between nest and food source. In acknowledgement of cooperation (synchronization) between fellow workers and hence less time spent at the food source (increased efficiency), the harmonic mean is preferred for time data (rates).

Unless otherwise stated, means are given with their 95% confidence interval (CI) using the standard error and two-tailed t distribution. As consumption per unit area is a linear projection of mound density (Meyer *et al.*, 1999), annual food consumption is reported as an overall mean based on density.

Results

Minor workers made up a small percentage of foraging workers, but with no apparent participation in ingestion. Other castes (notably soldiers) were ignored and not collected, as they do not fetch forage (i.e. ingest or remove litter).

Dry mass of the gut contents in a major worker was determined to be 1.483 ± 0.145 mg ($n = 10$) (Table 1) of which $42.4 \pm 2.3\%$ ($n = 5$) is ash. The proportion of food directly consumed by a foraging individual (stored in crop-gizzard) is $19.5 \pm 2.1\%$ ($n = 10$) of the ash-free material in the total gut (Table 2). A value of 0.166 mg is ultimately obtained, with a conservative CI of 0.009 mg.

The number of major workers foraging from small, medium and large colonies was estimated from previous studies to be $1\ 117 \pm 720$ ($n = 3$), $7\ 310 \pm 672$ ($n = 16$) and $45\ 329 \pm 12\ 014$ ($n = 16$), representing 35.5% of all workers in these colonies (Chapter 2; Meyer, unpublished).

The foraging period comprises approximately 12 hours (43 200 s) of a 24 hour day, and usually takes place nocturnally (Usher, 1975; Lepage, 1977; Ferrar, 1982; Meyer,

personal observation). It wasn't possible to get precise data for this variable, because this species is easily disturbed. As consumption depends on foraging distance (where litter occurs) and hence time spent away from the nest, estimates for different sized colonies (Chapter 2) are given at incremental distances (Table 3). Distances (radii) greater than 1 m extrapolated to occur between the mound and litter were verified by field observations.

Table 1. Dry mass of gut contents (incl. ash) of pooled major worker samples from foraging sites of ten *Macrotermes natalensis* colonies.

Dry gut contents (g)	Number of foraging major workers	Individual dry gut contents (mg)
0.1886	105	1.796
0.1033	85	1.215
0.2648	189	1.401
0.1004	65	1.545
0.6068	452	1.343
0.5221	382	1.367
0.3735	237	1.576
0.0962	78	1.233
0.5469	342	1.599
0.2665	152	1.753

Table 2. Dimensions and volume (± SD) of different sections of the digestive tract (uncoiled) of foraging *Macrotermes natalensis* major workers ($n = 10$).

Section	Length (mm)	Diameter (mm)	Volume (mm^3)
Crop-gizzard	1.5 ± 0.2	1.2 ± 0.2	1.21 ± 0.53
Midgut	6.4 ± 0.6	0.6 ± 0.1	1.91 ± 0.59
Proctodeum	2.2 ± 0.2	1.2 ± 0.3	2.79 ± 1.33
Colon	1.8 ± 0.2	0.4 ± 0.1	0.22 ± 0.12
Rectum	0.5 ± 0.1	0.5 ± 0.1	0.05 ± 0.03

By employing the given formula that I developed and using the values for all the variables mentioned, overall food consumption of *M. natalensis* in the northern KNP is estimated to be 20.19 ± 11.45 kg/ha/yr ($n = 20$ landscapes) established using dry, ash-free gut (crop-gizzard) contents.

Discussion

From the results I conclude that major workers ingest about 3–5% of dry body mass during foraging. Lepage (1977) found that the grass-feeding *Macrotermes subhyalinus* (Rambur) in Kenya ingests 6–8%, part of which may be protruding from

Table 3. Average time spent per individual ($n = 29$) during a foraging excursion from the mound to (and at) the food source (and back) and the resultant annual food consumption (based on harmonic time) of colonies of different sizes at incremental (extrapolated) foraging distances (radii) from the mound. (Variation is indicated by the 95% CI using the standard error and two-tailed t distribution and is accumulative for food consumption.)

Individual foraging time	1 m	5 m	10 m	15 m	20 m	25 m	30 m
Harmonic time (s)	38.2	191	382	573	764	955	1 146
Arithmetic time (s)	42.1 ± 4.4	210 ± 22	421 ± 44	631 ± 66	841 ± 88	1 052 ± 110	1 262 ± 132
Food consumption							
Small (kg/yr)	78.7 ± 63.6	15.7 ± 12.7	7.9 ± 6.4	5.2 ± 4.2	3.9 ± 3.2	3.1 ± 2.5	2.6 ± 2.1
Medium (kg/yr)	515.2 ± 131.3	103.0 ± 26.3	51.5 ± 13.1	34.3 ± 8.8	25.8 ± 6.6	20.6 ± 5.3	17.2 ± 4.4
Large (kg/yr)	3 195 ± 1 367	639.0 ± 273.5	319.5 ± 136.7	213.0 ± 91.2	159.7 ± 68.4	127.8 ± 54.7	106.5 ± 45.6

the mouth (visible in mandibles). Assuming a normal age distribution for the data used, young to old members should occur in a 1: 1 ratio (Odum, 1971). Then mainly the old workers of the major subcaste would be directly responsible for foraging duties (Oster & Wilson, 1978).

The farther that food is away from the nests (Table 3), the less consumption per unit time (foraging period) will be in the sense of litter moved into foci. This is evident in extensive denuded areas void of marked vegetation (removed by termites) often occurring around large mounds. As food becomes depleted close to the mound, foraging distances have to increase in order for workers to acquire food (Chapter 2).

Consumption of litter was previously studied by comparing the mass of food before and after it has been fed upon (e.g. Matsumoto & Abe, 1979; Collins, 1981c; Bagine, 1989). In some studies artificial bait was used, but that approach may not reflect the true rate of natural consumption (e.g. Usher, 1975; Buxton, 1981b). A common concern with regard to these studies is that the termites may not solely be responsible for litter removal. Hence the amount of litter removed by termites may be overestimated.

In the case of *M. natalensis*, presence of soil runways is related to soil moisture and cannot be used as indication of the amount of food consumed. Dry soils have more aboveground foraging runways than wetter soils. Burrowing is discouraged when soils are dry and hardened, thus encouraging the termites to surface and construct runways.

Collins (1981a), using a baiting technique, reported consumption of *Macrotermes bellicosus* (Smeathman) in Nigeria to be 225.91 kg/ha/yr, which is more than that of the present study (20.19 kg/ha/yr) by an order of magnitude. However, Collins' estimate is expressed as dry mass (incl. ash), whereas that of the present study excludes ash (albeit mostly attributed to sand in the gut). When using the biomass of *M. natalensis* for the northern KNP (0.51 kg/ha – Chapter 3) in conjunction with the consumption rate given in Nigeria (48.11 kg consumed/kg biomass/yr), I calculate consumption to be 24.53 kg/ha/yr for the study area. Given the different mound densities – 0.27/ha in KNP (Meyer *et al.*, 1999) and 6.45/ha for the Nigerian study

site (Collins, 1981a) – it is likely that this is responsible for the differences in quantities of food consumed at the different localities.

When the significant relationship found between litter production and rainfall (Collins, 1977) is used to predict litter production in the northern KNP based on annual rainfall (Dent *et al.*, 1987), I conclude that *M. natalensis* consumes 3.4% of the woody litter produced annually by comparison with 4.7% consumed by *M. bellicosus* (Collins, 1981a). Both regions are woodlands dominated by the pod-bearing Caesalpinioideae (Fabaceae), and it appears that these two allopatric species have similar roles in decomposition in their habitats.

Acknowledgements

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Chapter 5

DISCUSSION

Litter is conspicuously abundant in nutrient-poor savannas, such as the western granitic landscapes of the KNP, where termite-dominated soil fauna is abundant, insect populations are erratic, and mammalian herbivory is reduced. On nutrient-rich soils of the eastern basaltic plains, where termites occur to a lesser degree, soil fauna is generally low and dominated by ants (Scholes 1990).

The inclusion of termites in ecological models should be considered where they occur abundantly, such as in the northern parts of the KNP. Original data (Meyer 1997) can be considered moderate (non-extreme) in the light of the fact that the 1991/92 drought has passed and the 2000 floods have not yet occurred. The derived data therefore presented in this thesis serves as reliable baseline indicators against which future oscillations, in especially biomass, could be measured. Data is archived at the GIS lab of the KNP and on the mainframe of the University of Pretoria.

General linear modelling (Chapter 2) demonstrated that soldiers decrease proportionally between the intermediate (ergonomic) and advanced (reproductive) colony stages. This decline may be related to reduced surface area to volume ratios as mounds increase in size. By less exposure in surface area to sun and predators thermoregulation and defence of mounds are optimized. Disinvestment in soldiers benefits the colony in that worker proportions and hence nutrient cycling 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 is sustained. This means that caste proportions are relative to colony development. The main conclusion of Darlington (1984) was that if a nest is not fumigated before excavation, some emigration might occur. The effect of the ring-trenching technique (Appendices I, II) may be equivalent to fumigation in that it isolates the population. Emigration from nests was not evident in the present study, nor was the return of workers or soldiers from foraging passages. The finding that aboveground volume can be used in regression to estimate the population of mounds indicates that

there is a close relationship between the size of a colony's population and its construction activities.

Although workers are more abundant, more biomass gets diverted into soldiers (Chapter 3). There is therefore a considerable cost of defence (Oster & Wilson 1978). However, turnover of workers is faster because of seemingly greater soldier longevity (Bouillon 1970; Darlington 1991). Older workers forage 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. Due to larger body size and mass in *M. michaelseni* (Darlington 1991), biomass of the neuters (steriles) in large mounds is five times higher than that of *M. natalensis* in the KNP. No biomass estimations were made by Ferrar (1982a) for any species of *Macrotermes*. Only individual body mass of *M. natalensis* was measured on a microbalance and reported. Furthermore, no density estimates were given in order for the reader to calculate the biomass of this genus and species.

From both a landscape (Gertenbach 1983) and land type (Venter 1990) perspective on termite biomass, it is clear that *M. natalensis* occurs more profusely in areas of undulation. High relief, which augmented biomass in the area surveyed, is due to more valleys and hills.

High rainfall zones of the northern KNP are preferred by *M. natalensis*. Rainfall generally increases from north to south, and more litter occurs in the south than in the north. Litter production in the south is further supported by the fact that elephant occur in higher population densities in the southern region north of the Olifants River, as more branches are brought down from the tree canopy and added to the litter pool. While this scenario is currently beneficial for the production of termite forage, overpopulation of elephants, as has occurred in Tsavo National Park, Kenya (I.J. Whyte, Senior Scientist, KNP Scientific Services, South Africa, pers. comm.), may drive vegetation along the savanna continuum from woodland to grassland (bush decroachment). This would alter the termite assemblage from wood feeders dominated by *M. natalensis* to grass feeders dominated by *Hodotermes mossambicus*.

Constant grazing and reduction of fire intensity increase tree and shrub biomass. Because *M. natalensis* consumes woody litter, an increase in woody vegetation will be beneficial for this species. 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 higher 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.

I showed that a number of interrelated environmental factors influence termite biomass. Although a degree of heterogeneity occurs within landscapes, principal soil and vegetation patterns have been recognized. Major parameters such as geology, terrain morphology and woody vegetation are reflected in land types, 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 at landscape scale.

If for purposes of comparison the biomass of *M. natalensis* is related to that of the whole genus, this represents 36 % of macrotermitine biomass (excl. *Odontotermes*) in the northern KNP. The present study showed that biomass of *M. natalensis* is lower than that of *M. bellicosus* in Nigeria (Collins 1981) and *M. subhyalinus* in Senegal (Lepage 1974). It is 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.

It was concluded in Chapter 4 that *M. natalensis* consumes 3.4 % of the woody litter produced annually in the northern KNP compared to 4.7 % consumed by *M. bellicosus* in Nigeria (Collins 1981). Both regions are woodlands dominated by the pod-bearing Caesalpinioideae (Fabaceae), and it appears that these two allopatric species have similar roles in decomposition in their habitats. Africa has high termite diversity, increasing towards the tropics. The ability of termites to survive in fragmented habitats increases allopatric speciation where their dispersal is low (Brandl & Kaib 1995). This ability to survive is augmented by grouping (*K* strategy) and reproducing (*r* strategy).

Ferrar (1982b) made use of toilet rolls to determine foraging activity of termites. To his admission, consumption of toilet rolls would be difficult to relate to natural forage. He further reported that *Macrotermes* is active at deeper soil levels than other termites, and patchily so. Foraging occurs throughout the year. This is recognized in the present study by not using baiting techniques but relying on direct measurement of gut contents from foraging individuals and then using this data in my formula for determining annual food consumption on average.

Badertscher *et al.* (1983) confirmed Noirot's (1969) notion that there is a division of labour in the Macrotermitinae partly vested in caste. Almost 91 % of workers in a foraging party of *M. subhyalinus* are major workers. In the present study major workers of *M. natalensis* make up almost the entire worker force that goes out to forage. I have shown that termites contribute to litter fragmentation and the recycling of nutrients into the soil. The important role that termites play as primary decomposers has been demonstrated. Decomposing microbes are secondary receivers of carbon compounds fragmented by the termites. This interaction of passing on of nutrient-rich particles across a decreasing size spectrum enables the movement of nutrients through the terrestrial ecosystem (soil solum). As termites are generally soil-dwelling ectotherms, they are reliant upon properties of the soil solum. The Macrotermitinae are less dependent on these factors because of mound architecture and fungal symbiosis (*e.g.* Lee & Wood 1971; Fraser 1993; Korb & Linsenmair 2000). Termites are also able to patchily change soil properties in the environment (Pomeroy 1976, 1978).

These results will provide greater understanding of the ecology of *M. natalensis* in the northern KNP by bringing them into relation with studies of other components of the ecosystem. Soldier proportions of *M. natalensis* were found to be approximately 30 % (Chapter 2), whereas soldiers of *M. michaelseni* comprised little more than 4 % of the nest population (Darlington 1991). These species are sympatric in the northern KNP (*e.g.* Meyer *et al.* 1999), but phylogenetically divergent (Brandl & Kaib 1995; M. Kaib, pers. comm.) and consequentially different in colony development and caste composition. Basic data about the natural history of this species will benefit future monitoring projects on a macroecological scale. For instance, determining the genetic relatedness within and between colonies will provide greater understanding of the behavioural ecology, modes of reproduction and population viscosity of *M. natalensis*

in the northern KNP. This can be done via multilocus DNA fingerprinting using microsatellites (*e.g.* Kaib *et al.* 2000; Vargo 2000).

This thesis provides a set of data that can be used to evaluate the role that a particular species of termite plays in an important natural ecosystem. Analysis of colony composition, biomass and food consumption allowed for an assessment of the significance of this species in nutrient turnover. The results may be used to make comparisons with comparable termite assemblages elsewhere on the subcontinent. This is a major contribution to providing data on an invertebrate component of the ecosystem. Components such as this, are chronically overlooked in assessment programmes. It will allow defensible positions to be taken on invertebrate research in future and pave the way for further such work.

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APPENDIX I. Excavation of Mound 5 using ring-trenching and vacuuming techniques

APPENDIX II. Excavation of Mound F using ring-trenching and vacuuming techniques