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Miombo woodland termite mounds: resource islands for small vertebrates?

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Abstract

Macrotermes mounds are a significant feature of African woodland landscape, contributing to habitat heterogeneity. The mounds are massive, often many centuries old, and support dense vegetation and a suite of woody plant species scarce in surrounding woodland. The present study tested the hypothesis that Zimbabwean *Macrotermes* mounds, with their greater niche availability, were more heavily utilized by small vertebrates than the surrounding miombo woodland. We carried out a survey of amphibian, reptile and mammal species during early and late rains for 16 termite mounds and 16 adjacent woodland habitat sites, and compared numbers of individuals, species and diversity. For amphibians and reptiles, individual numbers and species did not differ significantly between habitats and their activity was more influenced by season. For mammals, however, significantly more individuals and species were captured on termite mounds, with three species captured only on mounds (most notably the musk shrew *Crocidura hirta* spp. complex) and all others showing marked preference for this habitat. The greater number of mammals on termite mounds contributed to total small vertebrate biomass being 800 g/ha for termite mounds compared with 380 g/ha in woodland. For mammals certainly, *Macrotermes* mounds provide significant food and habitat in miombo woodland.

Key words: diversity, frogs, lizards, *Macrotermes*, small mammals

INTRODUCTION

Members of the *Macrotermes* genus construct massive conical mounds, which are a significant feature of the landscape in African woodlands. Mound densities vary greatly depending on soil, geography and termite species, with figures of around five mounds/ha common (Pomeroy, 1977; Lepage, 1984; Meyer *et al.*, 1999). Some *Macrotermes* mounds reach 6 m in height and 30 m in diameter and consist of up to 27 m^3 of soil (Howse, 1970; Meyer *et al.*, 2000). Large mounds can be many centuries old and are potentially immortal through repeated colonisation (Watson, 1967; Lee & Wood, 1971; Moore & Picker, 1991). The area of influence of these mounds is correspondingly large, and their affect on the ecology of an area substantial. Their presence in the miombo landscape enables a good test of spatial heterogeneity models, in particular a test of the link between increased habitat heterogeneity and increased species diversity and carrying capacity.

Termites have a vital role in nutrient cycling, their mounds being eutrophic hot-spots in the otherwise homogeneous landscape (Frost, 1996). Mound soils have a higher pH, moisture, organic matter and minerals, including nitrogen, carbon, calcium, magnesium, potassium and phosphorous (Lee & Wood, 1971; Okello-Oloya, Spain & John, 1985; Pomeroy & Service, 1986; Okwakol, 1987). Unlike the mounds of most termite species, *Macrotermes* mounds support vegetation. The eutropic soil composition leads to a plant species composition that is distinct from surrounding woodland and includes species recognized as components of different biomes, such as riverine and rocky habitat (Burtt, 1942; Wild, 1952; Lee & Wood, 1971). Notably more termite mound species are evergreen, and coupled with elevated nutrient levels, mounds subsequently form islands of high vegetation density in otherwise open woodland (Burtt, 1942; Morrison, Hoyle & Hope-Simpson, 1948).

Termites are an abundant food source and an important dietary component of both generalist and specialist vertebrate species, while their mounds also provide suitable habitat for many species (e.g. Mitchell, 1965; Lee & Wood, 1971; Wood & Sands, 1978; Delany & Happold, 1979; Smithers & Wilson, 1979; Lynch, 1986; Jones, 1990; Kok & Hewitt, 1990; Linn & Key, 1996; Creel, 1997; Mills & Hes, 1997; Keesing, 1998). Burrows in termite mounds make particularly suitable nest areas, maintaining constant temperature and humidity (Lynch, 1986; Pomeroy & Service, 1986; Darlington, 1991). Furthermore, their height provides important vantage

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points for larger mammals (pers. obs.), while in vlei land vulnerable to water-logging, termite mounds may provide the only suitable dry ground (e.g. Cowles, 1926).

The first aim of the present study was to examine differences between termite mound and woodland vegetation. These data were a quantification of previous records of unique termite mound vegetation (Wild, 1952). The second aim was to determine whether *Macrotermes* mounds support a greater abundance and diversity of small vertebrates, and if there was any advantage conferred by this habitat that could be measured in terms of larger size or reduced home ranges. To test these hypotheses, we simultaneously surveyed amphibian, reptile and mammal species for 16 termite mounds and 16 adjacent woodland habitat grids and compared species presence as well as individual measurements.

The study was carried out in miombo woodland in Zimbabwe, dominated by *Brachystegia spiciformis* and *Julbernardia globiflora*, during early and late rains. To our knowledge, this is the first assessment of small vertebrate abundance and distribution on Macrotermitinae mounds, with other evidence of utilization confined to accounts of nesting or egg-laying for individual species. The only comparable survey of vertebrate species appears to be the work of Lynch (1986), although the *Trinervitermes trinervoides* mounds examined reach a maximum height of only 1 m and diameter of 2 m, and are not vegetated.

METHODS

Study sites

This study was carried out on 2 commercial farms in Zimbabwe, approximately 50 km apart. Cockington Estate (‘Cockington’) is located 70 km west of Harare while Carolina Wilderness (‘Carolina’) is located on the south banks of Lake Chivero, 40 km south-west of Harare. None of the areas examined has been used for commercial crops.

Termite mounds form a regular pattern in the miombo landscape, and are clearly visible in aerial photographs. Mound densities in the vicinity of areas studied were 1.26 ± 0.15 SD mounds/ha at Cockington and 1.44 ± 0.11 at Carolina (estimated from 4 counts of 0.25 km^2 from 1:50 000 aerial photographs; August 1996 and September 1997, Surveyor General’s Office, Harare). These densities are similar to those reported for *Macrotermes* mounds in South Africa (Meyer *et al.*, 1999) and Uganda (Pomeroy, 1977).

Eight termite mounds were selected at each farm either randomly, if many mounds were present, or by size (at least 2 m in height) when few mounds were present. Average dimensions were 3.4 ± 0.6 m height and 21.7 ± 2.7 m diameter at Cockington ($n = 8$), and 3.2 ± 0.7 m height and 24.1 ± 1.0 m diameter at Carolina ($n = 8$). The mounds examined were probably constructed by *Macrotermes falciger* or *M. natalensis*, and were structures typical of these species. Corresponding woodland habitat sites, between 20 m and 80 m away, were selected using random bearing and distance readings.

Vegetation analysis

Woody plant species were recorded for each woodland and termite mound site. Nomenclature followed Coates-Palgrave (1983), van Wyk & van Wyk (1997) and R. Drummond (pers. comm.). Correspondence analysis was conducted for the 74 plant species that were recorded from at least 3 sites; raw data were dominance (2), presence (1) and absence (0).

Vertebrate trapping

Trapping was carried out around the new moon in September–October 1999, during the first rains of the season and the hottest time of the year (hereafter referred to as ‘early’ season) and in January–March 2000, during the late rainy season (hereafter referred to as ‘late’ season). Times were selected to maximize trap success and the range of species encountered, but were also restricted by access difficulties due to high rainfall and flooding as well as civil disturbance.

The standard grid layout of 25 live box traps (baited with peanut butter and oats) and 2 pit traps (submerged 20 l buckets with 10 m drift fences of black polythene sheeting) covered an area of 0.25 ha. Four termite mounds and adjacent woodland grids were trapped simultaneously at any one time. Traps were open over 3 days and nights, and cleared in the early morning (also late afternoon in hot weather); a total of 5184 trap nights was carried out. Animals were identified (Smithers & Wilson, 1979; Broadley, 1988; Lamibris, 1989; Passmore & Carruthers, 1995; Stuart & Stuart, 1995; Branch, 1998), sexed, weighed, measured, and individually marked by toe-clipping[1] before release.

Numbers of individuals, total captures and species within woodland habitat and on termite mounds were calculated for each vertebrate taxon (amphibians, reptiles and mammals). These data were tested by 2-way ANOVA for the effects of habitat (woodland and termite mounds) and season (early and late).

The Shannon-Wiener diversity index (H) was calculated for each grid (Zar, 1996) and then treated as normally distributed data (Magurran, 1988): diversity indices were analysed by 1-way ANOVA for each taxon separately, as well as together, for the effects of season and habitat. The H statistic was also calculated for pooled taxa and grids in order to assess differences between seasons and habitats; this statistic and the derived degrees of freedom were compared by t-test, as given by Hutcheson (1970; cited by Zar, 1996).

For commonly caught species, animal weights (as well as total length for amphibians) were compared between woodland habitat and termite mounds by t-test. Individuals from each habitat were pooled and total biomass similarly compared by t-test.

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[1] The Ethical Committee of the Zoological Society of London considers that toe-clipping is no longer acceptable as a routine procedure for marking animals.

Data for woodland and termite mounds were averaged among the 16 grids for each habitat. Values are given as means ±1 SD throughout. Statistical analyses were carried out using STATISTICA software (Statsoft, 1995); the minimum level of significance was set at $P \leq 0.05$.

RESULTS

Vegetation analysis

There was little difference in numbers of woody plant species for woodland and termite mound sites, with 83 species recorded for woodland compared with 93 for termite mounds. However, substantial numbers of plant species were specific to either woodland or termite mounds: of the 74 species recorded on at least three grids, 20 were only recorded from woodland, while a further 20 were only recorded from termite mounds. Correspondence analysis revealed distinctly different vegetation species composition (ANOSIM, $P \leq 0.001$), with greater difference in vegetation composition between woodland sites and termite mounds within 20–80 m of each other, than the difference within habitat between the two farms, separated by around 50 km.

Species that dominated woodland habitat, but uncommon on termite mounds, include the miombo co-dominants *Brachystegia spiciformis* and *Julbernardia globiflora*, as well as *Burkea africana*, *Faurea saligna*, *Monotes glaber*, *Ochna pulchra*, *Parinari curatellifolia*, *Pseudolachnostylis maprouneifolia*, *Psorospermum febrifugum*, *Senna singueana*, *Swartzia madagascarensis* and *Vangueriopsis lanciflora*.

Species that were common on termite mounds, but uncommon in woodland, include *Albizia amara*, *Boscia angustifolia*, *Diospyros lycioides*, *Dombeya rotundifolia*, *Euclea divinorum*, *Flueggia virosa*, *Grewia flavescens*, *G. monticola*, *Strychnos potatorum*, and *Zizyphus mucronata rhodesica*. The majority of termite mound species (bar *Euclea*) have leaves that are eminently palatable to browsers, while a large proportion produce succulent (>70% water) or fleshy fruit. A small number of species (*Combretum molle*, *Dichrostachys cinerea*, *Lannea discolor* and *Lantana camara*) were recorded as common in both habitats.

Vertebrate trapping

Overall trap success was similar between woodland habitat and termite mounds in terms of numbers of individuals, species (Table 1, Fig. 1) and diversity (H calculated for pooled taxa: woodland sites $H = 0.57 \pm 0.18$, termite mounds $H = 0.67 \pm 0.14$). However, ANOVA indicated significant differences with season and habitat for the three vertebrate taxa (discussed separately below). In addition, species diversity was significantly higher for early trapping in both woodland (early $H = 1.12$, late $H = 0.84$, $t_{(139)} = 3.63$, $P \leq 0.001$) and termite mounds sites (early $H = 1.16$, late $H = 0.98$, $t_{(144)} = 3.12$, $P \leq 0.005$).

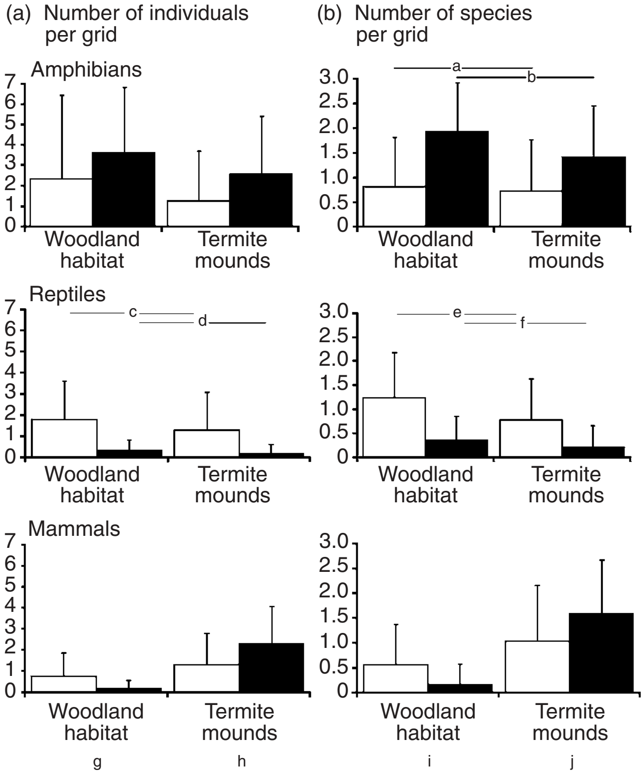

Fig. 1. Numbers of individuals (a) and species (b) of amphibians, reptiles and mammals captured in early and late trapping. Data are means ±1 SD averaged for 16 woodland habitat and 16 termite mound grids of 0.25 ha each. Letters link similar groups, which are significantly different from each other at $P \leq 0.05$. White bars, early season data; black bars, late season data.

Amphibians

Around two-thirds of all individuals captured in this study were amphibians (Table 1). Early season trapping coincided with the first rain storms of the season, at which time reasonable numbers of frogs were captured; the greater number of captures during the late rains, when juveniles were also observed, was therefore not statistically significant. However, there were significantly more frog species encountered in the late season ($F_{(1,60)} = 9.13$, $P \leq 0.005$, Fig. 1), with the shovel-footed squeaker (*Arthroleptis stenodactylus*) being joined by the mottled shovel-nosed frog (*Hemisus marmoratus*) as co-dominant species. Also noteworthy is the presence of puddle frogs (*Phrynobatrachus* spp.) in the late sampling, while sand frogs (*Tomopterna* spp.) were only captured in the early season, albeit in small numbers.

We encountered a greater number and variety of frog species for woodland habitat than on termite mounds (Table 1, Fig. 1), although this difference did not attain statistical significance. Twice the number of *A. stenodactylus*, and all records of the frogs (*Leptopelis*

Table 1. Summary of trapping results for 16 woodland grids and 16 termite mounds. Values are the total number of individuals of each species caught. Data are given for each species with data for time of the season considered separately (left hand columns) as well as for pooled temporal data (bold)

	Woodland			Termite mounds		
	Early	Late	**Both**	Early	Late	**Both**
Amphibians						
Arthroleptis stenodactylus	21	22	**43**	13	11	**24**
Breviceps mossambicus	2		**2**	1	1	**2**
Bufo gutturalis		4	**4**	2	2	**4**
B. maculatus	3	2	**5**	1	4	**5**
Cacosternum boettgeri				1		**1**
Hemisus marmoratus	2	21	**23**	1	20	**21**
Kassina senegalensis				1		**1**
Leptopelis bocagii	3	1	**4**			
Phrynobatrachus mababiensis		4	**4**			
P. natalensis		4	**4**		3	**3**
Schismaderma carens	1		**1**	1		**1**
Tomoptema cryptotis	3		**3**			
T. krugerensis	2		**2**			
No. individuals	**37**	**58**	**95**	**21**	**41**	**62**
No. species	**8**	**7**	**11**	**8**	**6**	**9**
Reptiles						
Agama aculeata armata	3		**3**			
Bitis arietans arietans	1		**1**			
Chamaeleo dilepis dilepis				1		**1**
Gerrhosaurus nigrolineatus	4	2	**6**	1	1	**2**
Ichnotropis capensis capensis	13	1	**14**	10		**10**
Kinixys belliana spekii	1		**1**			
Lygodactylus angolensis	1		**1**			
L. capensis	1		**1**			
Mabuya striata wahlbergii		1	**1**		1	**1**
M. varia		1	**1**			
Nucras taeniolata ornata				2		**2**
Panaspis wahlbergii	4		**4**	7		**7**
Rhinotyphlops mucruso		1	**1**	1	2	**3**
Unidentified Elapid snake	1		**1**			
No. individuals	**29**	**6**	**35**	**22**	**4**	**26**
No. species	**9**	**5**	**12**	**6**	**3**	**7**
Mammals						
Aethomys chrysophilus	4		**4**	3	8	**11**
Crocidura hirta spp. complex				2	9	**11**
Dendromus melanotis	1		**1**	2		**2**
D. mystacalis				1		**1**
Grammomys dolichurus				1		**1**
Graphiurus murinus		2	**2**	1	3	**4**
Mus minutoides	4		**4**	5	7	**12**
Paraxerus cepapi	2	1	**3**	6	10	**16**
Saccostomus campestris	1		**1**	1		**1**
No. individuals	**12**	**3**	**15**	**22**	**37**	**59**
No. species	**5**	**2**	**6**	**9**	**5**	**9**
Average for 16 woodland habitat sites and 16 termite mounds						
No. individuals			**9.3 ± 6.1**			**10.3 ± 6.5**
No. species			**5.1 ± 2.5**			**5.9 ± 2.1**

bocagii), *Phrynobatrachus mababiensis* and sand frogs, were for woodland habitat. There was no discernible habitat preference for the mottled shovel-nosed frog or toads (*Bufo* spp.), the only species captured frequently enough to allow such comparison.

No trend in amphibian diversity (H) was determined with habitat (woodland sites $H = 0.29 \pm 0.23$, termite mounds $H = 0.25 \pm 0.20$; $F_{(1,29)} = 0.274$, $P = 0.6044$).

Reptiles

Both numbers of individuals ($F_{(1,60)} = 15.61$, $P \leq 0.0005$) and species ($F_{(1,60)} = 16.42$, $P \leq 0.0005$) of reptiles were significantly different with season (Fig. 1). Fifty-one individuals of 12 species were captured during the early season compared with 10 individuals of five species in the late season. This result is probably a reflection of ambient temperature, with hot early trapping more favourable to reptile activity. Although not significant, woodland yielded greater numbers of individuals and species than termite mounds (Table 1).

There was no significant difference in reptile species diversity (H) between woodland and termite mounds (woodland sites $H = 0.18 \pm 0.21$, termite mounds $H = 0.11 \pm 0.17$; $F_{(1,24)} = 1.006$, $P = 0.3258$).

Mammals

Significantly more mammals ($F_{(1,60)} = 18.81$, $P \leq 0.0001$) of a greater number of species ($F_{(1,60)} = 18.36$, $P \leq 0.0001$) were captured on termite mounds than in woodland (Table 1, Fig. 1). Around 80% of mammal captures were from termite mounds, largely within 10–15 m of the mound centre. Three species were encountered only on termite mounds, and for musk shrews (*Crocidura hirta* spp. complex), all 11 individuals encountered were from mounds. Seasonal differences in mammal captures were not significant, with similar numbers for each trapping session. However, there was a distinct difference in the distribution of captures between seasons, with more mammals captured in woodland during the early than the late season, and the converse holding true for termite mounds (Fig. 1).

Numerous burrows in mounds were observed, in active mounds as well as those with no obvious above-ground termite activity. Burrows that were probably used by mammals ranged in size from around 40 mm in diameter, to large 200–300 mm burrows produced by aardvarks and warthogs. Some red veld rats (*Aethomys chrysophilus*) ran straight into burrows in termite mounds upon release while tree squirrels (*Paraxerus cepapi*) similarly ran into hollows in trees growing on mounds.

Diversity indices, calculated for each grid separately and then analysed as normally distributed data (Magurran's method), were higher for termite mounds than woodland. Small numbers of mammals in woodland resulted in diversity figures of zero for many grids: of the 10 woodland grids where mammals were captured, only two included captures of more than one species. Therefore, although analysis by Magurran's (1988) method yielded a statistically significant result ($F_{(1,24)} = 11.86$, $P \leq 0.002$), the validity of this result may be doubtful. For diversity values calculated for grids pooled within each habitat (Hutcheson, 1970), the greater diversity value for termite mounds ($H = 0.75 \pm 0.04$) was not significantly greater than that observed for woodland habitat ($H = 0.69 \pm 0.06$, $t_{(31)} = -0.821$, NS).

Effect of habitat upon average size and total biomass of animals captured

For the two most commonly captured frog species, weights and snout–vent lengths were slightly larger for woodland than termite mounds. However, neither for the shovel-footed squeaker *A. stenodactylus* (woodland, termite mounds: $n = 42, n = 20$; $t_{(52)} = 1.356$, $P = 0.090$) nor mottled shovelnosed frogs *H. marmoratus* ($n = 20, n = 20$; $t_{(35)} = 1.684$, $P = 0.051$), were the differences in weights significant.

Although *Ichnotropis capensis* captured on termite mounds ($n = 8$) were marginally heavier than those encountered in woodland ($n = 15$), this difference was not significant ($t_{(11)} = -1.098$, $P = 0.148$). No other reptile species was captured in sufficient numbers to make a similar comparison.

Due to low numbers of mammals in woodland habitat, comparison of mammal weights and measurements between habitats was not possible.

Although there was no significant difference in the overall numbers of animals captured in woodland habitat and on termite mounds, there was a difference in the overall mass of animals captured, with termite mounds (800 ± 650 g/ha) yielding twice the mass of woodland (380 ± 340 g/ha, $t_{(15)} = 2.09$, $P = 0.054$).

DISCUSSION

The presence of *Macrotermes* mounds has a significant affect on miombo habitat, adding to overall heterogeneity and complexity. The presence of *Macrotermes* mounds clearly increases overall biodiversity as well as carrying capacity of the Zimbabwean miombo. More than a quarter of the total plant species recorded in the present study were from *Macrotermes* mounds and were not recorded in adjacent woodland. This supports Wild's (1952) observation that of the 62 species of plants he recorded from *Macrotermes* mounds, over half are important constituents of woodland in warmer and drier (low altitude) areas, or else are only otherwise found in rocky or riverine habitats. Conversely, we recorded woodland species that were absent from the mounds; presumably these are plants that are well adapted to the oligotrophic soils present in woodland habitat; their absence from termite mounds may reflect a poor ability to compete with nutrophilic and mesophilic species on mound soils.

Our hypothesis that this patchiness would increase niche availability, promoting small vertebrate species diversity (MacArthur & MacArthur, 1961; August, 1983; Huston, 1994) yielded some significant results. *Macrotermes* mounds are clearly supporting substantial numbers of small mammals due to either the provision of additional food resources or shelter, further increasing overall biodiversity.

As food for insectivores, in addition to termites, unique termite mound vegetation may also support insect species not otherwise found in the miombo. The musk shrew *C. hirta* spp. complex, woodland dormouse *Graphiurus murinus* and pouched mouse *Saccostomus campestris*, caught in the present study are all insectivores including termites in their diets (Roberts, 1951; Smithers & Wilson, 1979). Succulent and fleshy fruit produced by termite mound plant species may also provide food for granivorous and frugivorous animals. For example, Smithers (1983) lists *Acacia* spp., *Sclerocarya caffra* (marula), *Grewia* spp. and *Ziziphus mucronata* as components of the diets of the red veld rat *A. chrysophilus*, whilst the diet of the tree squirrel *P. cepapi* includes *Acacia* spp., *Ficus* spp., *Colophospermem mopane* and *Z. mucronata* (Viljoen, 1975; cited by Rautenbach, 1982). When present, the above plant species were recorded from termite mounds in this study, very rarely were they noted in woodland habitat.

Termite mounds may provide substantial shelter for animals; the dense spinescent plants provide protection from aerial as well as terrestrial predators, whilst the high proportion of evergreen species means that some protective cover is maintained throughout the year. In addition, nesting in termite mounds has been demonstrated for a number of mammal species and was supported by numerous burrows observed. The lesser dwarf shrew *Suncus varilla* for example, may be dependent upon termite mounds and is rarely found other than through excavations of such (Rautenbach, 1982; Lynch, 1986). We similarly captured all musk shrews on termite mounds; their presence may reflect use of burrows in termite mounds (Smithers, 1983) or else dependence upon dense cover (Smithers & Wilson, 1979). Our observations of the red veld rat confirms previous records of their use of burrows in termite mounds (Roberts, 1951; Smithers, 1983) and is also consistent with their requirement for dense cover (Smithers & Wilson, 1979). Furthermore, tree squirrels make heavy use of the trees growing on termite mounds and they are believed to be less common in miombo (*Brachystegia*) woodland compared with other habitats, primarily due to the presence of fewer tree hollows (Smithers, 1983; Linn & Key, 1996).

The observed seasonal variation in mammal captures between habitats may reflect differences in resource availability. More mammals were captured in woodland habitat during the early season than the late season, possibly reflecting greater abundance of grass seeds, which with summer rains may have subsequently germinated. By contrast, for termite mounds, the greater number of captures in late compared with early season may reflect recruitment of juveniles around nest sites (juveniles were trapped), or else recruitment to seasonally-available fruit or other food.

The present data gave no indication of preferential use of termite mounds by amphibians and reptiles. In fact, contrary to our hypothesis, twice the numbers of shovel-footed squeakers were captured in woodland than on termite mounds, whilst the small numbers of *Leptopelis bocagii*, puddle frogs and sand frogs were encountered only in woodland. Such preference may be related to soil structure and burrowing habit of these species, with termite mound soils too hard to enable these animals to burrow in their normal manner. By contrast, toads, which were reasonably evenly distributed between woodland habitat and termite mounds, use existing holes. Some amphibian species doubtlessly shelter within the mounds, with a number of species captured in the present study also recorded for *Trinervitermes* mounds (Lynch, 1986). The fact that smaller frogs were found at termite mounds may tentatively suggest that the clay soils of termite mounds may be more suitable habitat for breeding compared with sandy soils of the surrounding woodland (Lee & Wood, 1971; Wood & Sands, 1978) where freestanding water may be scarce.

Published habitat preferences suggest that reptiles may make more use of termite mounds than has been indicated in the present study (e.g. Cowles, 1926; Cogger, 1959; King & Green, 1979; Carlzen, 1982; Wells & Wellington, 1985; Lynch, 1986; Branch, 1998; Hoser, 1998). Several blind snakes *Rhinotyphlops mucruso* were captured in the present study; these animals feed mainly on a diet of termites, burrowing into termite mounds to feed, only emerging when heavy rains saturate their burrows (Broadley, 1988; Branch, 1998). Although three individuals were recorded from termite mounds, a single individual was also captured in woodland habitat after exceptionally heavy rain. Species like the snake-eyed skink *Panaspis wahlbergii* may prefer termite mounds for their greater amount of leaf litter, the numbers recorded in this study are not conclusive and requires further trapping. The numerous snakes reported by Lynch (1986) were captured through excavation and therefore unlikely to be caught in the traps used in this study, although some were observed entering termite mound burrows.

Termite mounds yielded approximately twice the small vertebrate biomass of woodland habitat, and therefore provide a greater resource for higher levels of the food chain. This difference could be due to an increase in primary productivity associated with greater nutrient availability on termite mounds (Banerjee & Mohan, 1976; Okwakol, 1987; Holt & Coventry, 1990) although the link between productivity and animal diversity is a complex issue (Rosenzweig, 1995). Small vertebrate biomass for woodland is also similar, while the figure for termite mounds is almost double that recorded for miombo woodland at Sengwa, Zimbabwe (Linzey & Kesner, 1997*b*). Mammal diversity indices (*H*) encountered in the present study are comparable to figures given by Linzey & Kesner (1997*b*), although the composition of the small mammal communities is vastly different (Linzey & Kesner, 1997*a*). For example, the scarcity of shrews and pygmy mice *Mus minutoides* in their study may reflect that no trapping was carried out on termite mounds, nor were pit traps used. They also captured many bushveld gerbils *Tatera leucogaster*, which were not recorded in the present study.

We could not generate enough data to test the hypothesis that home ranges were affected by the presence of termite mounds. However, given the close proximity of woodland grids to termite mounds, the fact that so few mammals were captured in woodland suggests that some mammals may rarely move away from the mounds. This finding agrees with Viljoen's (1997) observation that tree squirrels will often spend the entire day feeding in only 150 m^2 and that their territories in termite mound thickets varies between 0.3 and 1.26 ha, consistent with a single mound included per territory. Further comparison of home-range size in areas without termite mounds would be valuable.

Conclusion

Termite mounds have long been described as nutrient hot-spots in a more oligotrophic matrix (Wood & Sands, 1978; Okello-Oloya *et al.*, 1985; Okwakol, 1987), this study further demonstrates that termite mounds also act as a significant resource for small mammals. The presence of termite mounds in the miombo has a marked influence on mammal abundance and activity, as well as implications for higher levels in the food chain. Termite mounds should clearly be considered a focus of conservation importance and their destruction and utilization for farming (Nyamapfene, 1986) detrimental to a diverse range of plant and animal species, with a negative effect upon overall biodiversity of an area.

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