Habitat preferences of small mammals in the Katavi ecosystem of western Tanzania

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Abstract

We sampled small mammals in numerous habitat types throughout the wet and dry seasons in and around Katavi National Park, a remote protected area in western Tanzania consisting of miombo woodland and seasonal floodplains. Although trap success was relatively low (6.6%), a minimum of 23 species were caught in over 11,000 trap nights. These were *Crocidura hirta*, *Crocidura luna*, *Saccostomus campestris*, *Dendromus mystacalis*, *Steatomys pratensis*, *Tatera boehmi*, *Tatera leucogaster*, *Acomys spinosissimus*, *Aethomys chrysophilus*, *Aethomys kaiseri*, *Arvicanthis niloticus*, *Grammomys dolichurus*, *Lemniscomys rosalia*, *Lemniscomys striatus*, *Mastomys natalensis*, *Mus musculoides*, *Mus triton*, *Pelomys fallax*, *Graphiurus murinus*, *Petrodromus tetradactylus* and probably *Crocidura nanilla*, an unidentified species of *Mus*, and an unidentified rodent species. Overall species richness and abundance did not differ between wet and dry periods of the year. There were few differences in species richness between major habitat types but relative abundance was the highest in cultivated landscapes. Species communities differed between habitats and detailed environmental measures showed that species were more diverse and lived at greater abundance in taller vegetation. Species-specific habitat preferences uncovered here extend a number of findings from several earlier studies in miombo woodland. This study highlights the importance of taking quantitative measures of vegetation at both coarse and fine scales, and the necessity of trapping across a wide variety of habitats.

Key words: biodiversity, habitat preferences, rodents, Tanzania

Résumé

Nous avons récolté des échantillons de petits mammifères dans de nombreux types d'habitats, en saison sèche et en saison des pluies, à l'intérieur et autour du Parc National de Katavi, une aire protégée éloignée de l'ouest de la Tanzanie composée de forêt de miombo et de plaines inondables. Bien que le taux de réussite par piège ait été relativement faible (6.6%), un minimum de 23 espèces ont été capturées en plus de 11.000 nuits-pièges. Ce sont Crocidura hirta, C. luna, Saccostomus campestris, Dendromus mystacalis, Steatomys pratensis, Tabera boehmi, T. leucogaster, Acomys spinosissimus, Aethomys chrysophilus, A. kaiseri, Arvicanthis niloticus, Grammomys dolichurus, Lemniscomys rosalia, L. striatus, Mastomys natalensis, Mus musculoides, M. triton, Pelomys fallax, Graphiurus murinus, Petrodromus tetradactylus et, probablement, C. nanilla, une espèce non identifiée de Mus et une espèce non identifiée de rongeur. En général, la richesse et l'abondance des espèces ne différaient pas entre saison sèche et saison des pluies. Il y avait peu de différence de la richesse en espèces entre les principaux types d'habitats, mais l'abondance relative était plus élevée dans les paysages cultivés. Les communautés d'espèces différaient selon les habitats, et des mesures environnementales détaillées ont montré que les espèces étaient plus diverses et vivaient en plus grande abondance dans une végétation plus haute. Les préférences de l'habitat spécifiques des espèces découvertes ici s'ajoutent encore au nombre de découvertes réalisées lors d'études antérieures dans la forêt de miombo. Cette étude souligne qu'il est important de prendre des mesures quantitatives de la végétation, à une échelle grossière mais aussi plus fine, et qu'il est nécessaire de faire les piégeages dans une grande variété d'habitats.

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Introduction

Our current understanding of the habitat preferences of rodents and insectivores in Africa is weak because studies have been conducted in different ecosystems, each with different study objectives, methodologies and lengths of study periods (e.g. Delany, 1971; Cole, 1975; Cheeseman & Delany, 1979; Iwaye, 1989; Stephenson, 1993; Sillero-Zubiri, Tattersall & Macdonald, 1995; Keesing, 1998; Granjon *et al.*, 2002). Moreover, findings are confounded by the restricted geographical focus of the majority of studies with many large areas receiving little or no attention. For example, although many studies have investigated the rodent ecology of the miombo–mopane woodlands of southern-central Africa area, most have given only brief consideration to habitat preferences, focusing instead on other issues such as population dynamics (Sheppe, 1972; Happold & Happold, 1990, 1991; Liers *et al.*, 1997), growth trajectories of specific species (Liers *et al.*, 1990; Christensen, 1993), small mammal behaviour (Choate, 1972; Hubbard, 1972), reproduction (Neal, 1991), community structure (Linzey & Kesner, 1997a) and conservation (Happold & Happold, 1997). In those few studies that do discuss habitat preferences in this biome there is surprisingly little consensus, making generalizations difficult.

Although almost two-thirds of Tanzania is covered by miombo, and thus falls in a region identified as one of the Earth's last remaining vast wilderness areas (Mittermeier *et al.*, 2003), very few studies of rodents have been undertaken in this area of the country. Preliminary studies of the rodents in and around Katavi National Park, in western Tanzania, undertaken by TC between 2000 and 2001, focused on differences in species composition and abundance between different levels of area protection (Caro, 2001, 2002). These studies suggested that species richness and abundance were higher outside Katavi National Park than inside. While environmental factors were given some attention in these studies – trap grids were set up in a variety of different habitats in each sort of protected area, and measures of cover, vegetation and predator abundance were taken – no systematic attempt was made to examine whether different species were found in different habitats or whether species' abundances varied across different environments. In addition, voucher specimens were not taken and so a true species list could not be drawn from these studies as specimens might have been misidentified in the hand. The primary objectives of the present study, conducted during 2002–2003, were to build upon the preliminary studies by providing a verified species inventory for this little known area of East Africa (but see Vesey-Fitzgerald, 1966), to analyse how species composition and abundance vary between broad ecological habitats, and to describe species' microhabitat preferences in an effort to quantify habitat requirements of different small mammal species living in the miombo–mopane biome.

Methods

The study was conducted within and around Katavi National Park (latitude 6°45′–7°05′S, longitude 30°45′–31°25′E) in Mpanda District, Rukwa Region at the north end of the Rukwa Valley, western Tanzania (Fig. 1) between August 2002 and April 2003 (Caro, 1999). The area consists largely of miombo woodland, a dry deciduous forest characterized by the family Fabaceae and *Combretum* and *Terminalia* species (Rodgers, 1996; T. Banda, pers comm). Three large seasonally flooded grasslands (mbugas) are found in the western half of the Park where we worked, with smaller mbugas found within surrounding uncultivated areas. The majority of permanent settlements are found south of the Park where land use consists primarily of maize and rice cultivation, cattle grazing and firewood collection. The area generally experiences a single dry season from May to October and a wet season from November to April. Total rainfall during the study period was 746 mm but the wet season was abnormal, however, with almost no rain falling during February and relatively little in April.

EF and TG sampled a total of 41 separate sites covering an area of approximately 2500 km^2 both within and outside the Park (Fig. 1). The majority of sites were re-sampled either once or twice again during three time periods: dry (August–October), intermediate (November–January) and wet seasons (February–April). Each site was trapped using 30 Sherman traps divided between six trapping clusters, each consisting of five traps, distributed across an area of approximately 0.25 km^2. Each trap cluster was restricted to an area approximately 20 m in diameter, and each cluster was spaced a minimum of 50 m apart. Traps were always baited with peanut butter (Laurance, 1992; Woodman *et al.*, 1996) and were checked and rebaited each morning for four or five consecutive trap

Fig 1 Map of the study area showing Katavi National Park and neighbouring areas in Rukwa Region, western Tanzania. The boundaries of Katavi National Park, Msaginia Forest Reserve, and Mlele Game Controlled Area are shown; Usevya Open Area lies to the south of the Park. Major seasonal floodplains are shown as darker shaded areas. Exclamation points identify the 41 study sites. Locations for all sites are accurate to 100 m. Research was based out of Kibaoni
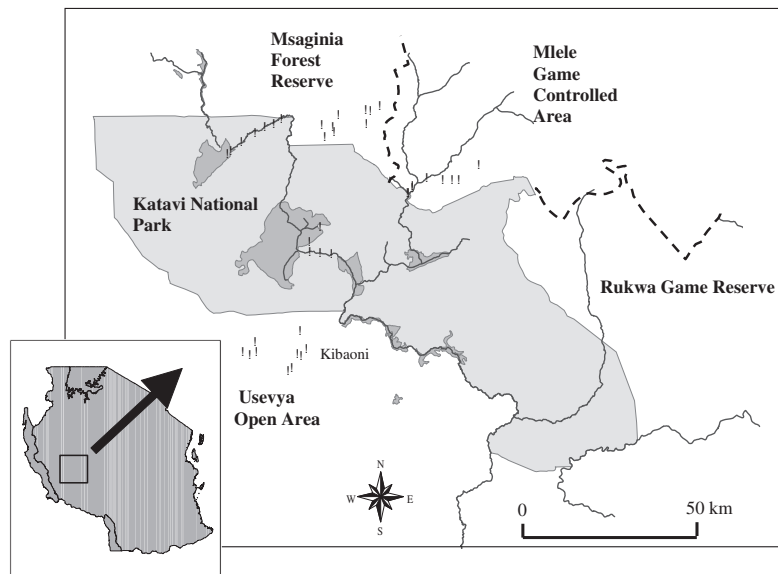
nights per site (equalling a total of 120–150 trap nights per site for any one trapping session).

Captured individuals were either marked with a permanent ink pen, the colour of which lasted a minimum of 24 h but usually longer, and released or taken as voucher specimens using chloroform as required (where trap success allowed, we took a minimum of four voucher specimens of each rodent type depending upon interspecies variation). Skulls and skins were later formally identified by PJ. At each site, we calculated standardized small mammal species richness as the number of different species captured per trap night (Nichols & Conroy, 1996) to enable direct comparisons to be made with earlier trapping studies in the same area, and abundance as the number of captures of different individuals divided by the number of trap nights (Krebs, 1999; Magurran, 2004). Less attention was paid to insectivores, and although a sample of speci-

mens was collected, the majority of captures were recorded simply as shrews and released following marking.

We stratified our study sites with respect to six composite habitat categories: wooded riverine, open riverine, mbuga (seasonal floodplain), cultivated, open woodland and closed woodland (Table 1). We also took detailed vegetation and other environmental measurements at the microhabitat scale at each trap cluster. These were: (1) percentage vegetation cover (estimated from a circle with a radius of 5 m around the centre of the trap cluster) using five categories (bare ground, leaf litter, herbaceous cover, shrub cover and tree cover) broken into an ordinal scale where 0% = 1, 1–20% = 2, 21–40% = 3, 41–60% = 4, 61–80% = 5 and 81–100% = 6. (2) Height of herbaceous vegetation on a five-point ordinal scale where 0 cm = 1, 1–20 cm = 2, 21–50 cm = 3, 51–100 cm = 4 and >100 cm = 5. For all these measures, a mean was taken from across the six

Table 1 Major habitat categories within the Katavi Ecosystem

	Canopy cover (%)	Canopy height (m)	Under-story	Remarks
Wooded riverine	>30	5–15	Sparse	Seasonal or perennial river with woodland within 10 m of each bank
Open riverine	10–50	5–10	Sparse	Seasonal or perennial river with woodland on one side only
Open woodland	2–30	0–5	Very dense	Low canopy wooded savannah (open woodland and grassland mosaic), usually with dense under-story foliage
Closed woodland	>30	5–15	Dense	Mature miombo woodland characterized by relatively tall trees and an open under-story
Mbuga	0	0	Open	Seasonally flooded open grassland
Cultivated	0–80	0–5	Variable	An agricultural landscape dominated by maize, bananas, cassava, peanuts and sugar cane

trap clusters to provide an overall measure for each environmental variable at each site. (3) Distance to the nearest water source measured on an ordinal scale from the centre of the trap cluster (minimum value taken from across the year) where <10 m = 1, 10–20 m = 2, 20–50 m = 3, 50–100 m = 4, 100–500 m = 5 and >500 m = 6.

Results

Over 11,010 trap nights, we caught 732 different individual mammals comprising nineteen species of Rodentia, one species of Macroscelidea, and three species of Lipo-

typhla (Table 2). PJ identified voucher specimens to species level with the exception of two which could only be identified to the level of *Mus (Nannomys)*, and one that remains unidentified leaving open a possibility that it is new to science. Unfortunately, this cannot be confirmed as the specimen is unique and in relatively poor condition. Lacking biochemical and chromosomal data, specimens identified provisionally as *Mastomys natalensis* Smith, 1834 may represent other species belonging to the genus, which is in need of revision (Musser & Carleton, 1993).

Of the species that we caught, none constituted range extensions with the possible exception of *Crocidura nanilla*

Table 2 Small mammals captured in this study (based on Wilson & Cole, 2000) and number of individuals of each species captured per 100 trap nights separated by habitat categories

		N[a]	A	B	C	D	E	F
Order Lipotyphla								
Family Soricidae		93	0.50[b]	0.42	0.65	2.44	0.50	0.49
Crocidura hirta	Lesser red musk shrew							
Crocidura luna	Greater grey-brown musk shrew							
Crocidura nanilla?	Tiny white-toothed shrew							
Order Rodentia								
Family Muridae								
Saccostomus campestris	Pouched mouse	36	0	0.28	0.74	0	0.17	0.40
Dendromus mystacalis	Chestnut climbing mouse	2	0	0	0	0	0	0.01
Steatomys pratensis	Fat mouse	15	0.01	0.54	0	0	0.17	0.01
Tatera boehmi	Boehm's gerbil	5	0	0	0.10	0	0.17	0
Tatera leucogaster	Bushveld gerbil	15	0.10	0	0	0.91	0	0
Acomys spinosissimus	Spiny mouse	4	0.25	0	0	0	0.01	0
Aethomys chrysophilus	Red rock rat	78	0.52	0	0.65	1.59	1.08	0.35
Aethomys kaiseri+	Kaiser's rock rat							
Arvicanthis niloticus+	African grass rat							
Grammomys dolichurus	Woodland thicket rat	13	0.08	0	0.17	0.01	0.22	0.19
Lemniscomys rosalia	Single striped grass mouse	20	0.33	0.12	0.01	0.16	0.33	0.19
Lemniscomys striatus	Typical striped grass mouse	29	0.01	0.01	0.01	0.24	1.20	0.01
Mastomys natalensis	Natal multimammate mouse	325	0.75	1.25	0.81	11.81	2.67	0.88
Mus musculoides	Temminck's mouse	36	0.33	0.01	0.14	0	0.67	0.69
Mus triton	Grey bellied pigmy mouse	36	0	0	0.55	0	0.61	0.22
Mus	unidentified	2	0	0	0.01	0	0	0
Pelomys fallax	Creek groove-toothed swamp rat	2	0.01	0	0	0	0.01	0
Family Myoxidae								
Graphiurus murinus	Woodland dormouse	20	0	0	0.46	0	0.01	0.35
Unidentified rodent		1						
Order Macroscelidea								
Family Macroscelididae								
Petrodromus tetradactylus		1	0	0	0	0	0	0.01
Four-toed elephant shrew								

A, Wooded riverine; B, Open riverine; C, Floodplain; D, Cultivated; E, Open woodland; F, Closed woodland.
[a]Total number of individuals captured in Sherman traps.
[b]All species of insectivores combined.
+ Not captured in a Sherman trap.

Thomas, 1909 recorded by Hutterer (1993) as being distributed in 'dry and moist savannah from West Africa (Mauritania) to Kenya and Uganda; perhaps further south'. Our species list taken from a period spanning dry and wet seasons (August–April) is unlikely to be exhaustive because the rate of new captures of small mammals was still increasing at the end of the study (Fig. 2).

Taking all our sites together, we found no significant differences in species richness or relative abundance between seasons when all species were combined (rodent species richness, Kruskal–Wallis tests, $H = 2.565$, df = 2, NS; rodent abundance, $H = 1.992$, df = 2, NS; small mammal abundance, $H = 1.617$, df = 2, NS). Therefore, we combined all trapping sessions at a given site in subsequent analyses. Nonetheless, when species were examined individually, we found that *Mus triton* Thomas, 1909 and *Tatera leucogaster* Peters, 1852 were trapped more commonly in the dry season ($H = 7.145$, df = 2, $P = 0.028$; $H = 13.401$, df = 2, $P = 0.001$ respectively), *Aethomys chrysophilus* de Winton, 1897 was more common in the intermediate season ($H = 9.989$, df = 2, $P = 0.007$) and *Graphiurus murinus* Desmarest, 1822 in the wet season ($H = 7.794$, df = 2, $P = 0.020$).

We found no significant difference in rodent species richness across the composite habitat categories (Table 1, $H = 7.884$, df = 5, NS). In contrast, small mammal abundance differed across habitat categories: there was a significant overall difference among the six habitats
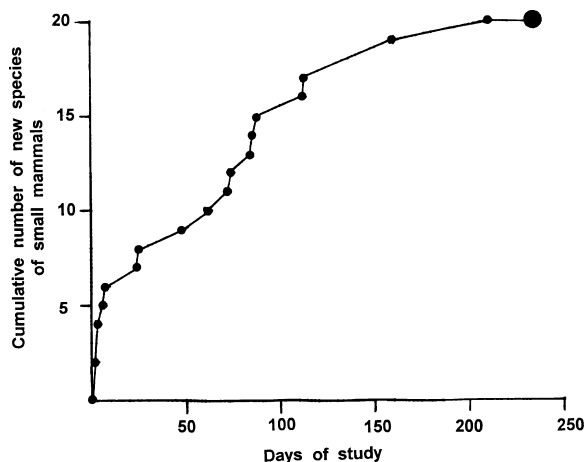
Fig 2 Species accumulation curve showing the number of new species of small mammals captured plotted against days spent in the field. Insectivores were excluded because they were not identified to species level. Large dot denotes termination of study

($H = 17.472$, df = 5, $P = 0.004$) with by far the most individuals being caught in cultivated landscapes (versus wooded riverine, Mann–Whitney *U*-tests, Ns = 6.5, U = 0, $P = 0.006$; versus open riverine, Ns = 6.7, U = 0, $P = 0.003$; versus floodplain, Ns = 6.9, U = 6, $P = 0.013$; versus closed woodland, Ns = 6.9, U = 4, $P = 0.007$) and in open woodland (versus wooded riverine, Ns = 5.5, U = 2, $P = 0.032$; versus open riverine, Ns = 5.7, U = 1, $P = 0.007$; versus closed woodland, Ns = 5.9, U = 6.5, $P = 0.033$; Fig. 3). Specifically, there were significant differences in numbers of *M. natalensis* and *A. chrysophilus* captured in different habitats ($H = 16.062$, df = 5, $P = 0.007$; $H = 16.654$, df = 5, $P = 0.005$ respectively) with more in cultivation than elsewhere (Table 2). However, there were no other significant differences between habitat categories when species were examined individually.

Measures of rodent species richness, rodent abundance and overall abundance of all small mammals were significantly related to vegetation height (Spearman rank correlation coefficients, n = 41 sites, $r_s = 0.399$, $P = 0.010$; $r_s = 0.512$, $P = 0.001$; $r_s = 0.483$, $P = 0.001$ respectively). Small mammals clearly preferred taller vegetation. Other environmental measures were not significantly associated with species richness or abundance of all species together.

Nonetheless, when habitat preferences of different species were examined at this fine level, restricting analyses to those for which we had fifteen or more captures, the following patterns emerged. *Saccostomus campestris* Peters, 1846 abundance was significantly correlated with meas-
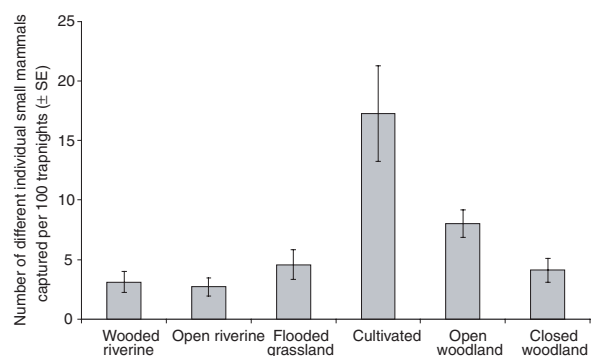
Fig 3 Mean number (and SE) of different individuals captured per 100 trap nights in six different composite measures of habitat. Numbers of sites in each habitat type: five in wooded riverine, seven in open riverine, nine in flooded grassland, six in cultivated, five in open woodland, nine in closed woodland

ures of leaf and tree cover (n = 41 sites for this and subsequent species, $r_s = 0.331$, $P = 0.035$; $r_s = 0.402$, $P = 0.009$ respectively). *Tatera leucogaster* individuals were more likely to be found where herb and tree cover were low ($r_s = -0.365$, $P = 0.019$; $r_s = -0.356$, $P = 0.022$). *Lemniscomys striatus* Linnaeus, 1758 abundance was negatively associated with distance to water ($r_s = -0.394$, $P = 0.012$) but positively correlated with vegetation height ($r_s = 0.549$, $P < 0.001$). *Mus musculoides* Temminck, 1853 numbers were negatively associated with shrub cover ($r_s = -0.357$, $P = 0.022$). Unsurprisingly, abundance of the arboreal *G. murinus* was significantly correlated with increasing leaf and tree cover and they preferred to be close to a water source ($r_s = 0.381$, $P = 0.014$; $r_s = 0.370$, $P = 0.017$; $r_s = 0.339$, $P = 0.032$ respectively). These were the only significant correlations between species trap success and microhabitat measurements.

Discussion

By taking voucher specimens, this study provides an important verification of species identified in the hand in previous studies in the same area (Caro, 2001, 2002). In those studies species identified as *M. natalensis*, *L. striatus*, *S. campestris*, *Rattus rattus* Linnaeus, 1758, and *G. murinus* were correctly identified all being highly distinctive species. *Aethomys chrysophilus*, however, was incorrectly identified as *Tatera leucogaster*; *Tatera leucogaster* or *Tatera boehmi* Noack, 1887 was incorrectly identified as *T. robusta* Cretzschmar, 1826; *Lemniscomys rosalia* Thomas, 1904 incorrectly as *L. griselda* Thomas, 1904; *M. triton* as *Myomys fumatus* Peters, 1878; *Arvicanthis niloticus* Desmarest, 1822 as *Dasymys incomtus* Sundevall, 1847; and *M. musculoides* as *Mus minutoides* Smith, 1834; however, the *M. minutoides – musculoides* complex is in need of revision, the precise geographical boundaries are unknown. The earlier studies as well as this one failed to check whether individuals classified as *Crocidura hirta* Peters, 1852 comprised of only *C. hirta* or a number of other shrew species as well. Therefore, all the species caught in earlier studies in and around Katavi were captured in this study with the exception of *R. rattus*; an exotic species which was caught exclusively in houses not sampled here. The three studies of small mammals in this area of Tanzania therefore constitute an important lesson in the importance of taking voucher specimens to check against a reference collection. More generally, they highlight the

need to sacrifice a small number of animals for correctly interpreting the ecology and natural history of a region.

This study found that at least nineteen species of rodent, three species of shrew and one elephant shrew live sympatrically in this area. Although species misidentifications occurred in earlier studies, the number of different morphotypes captured standardized by trapping effort was similar across years: 0.26/100 trap nights (n = 3106 trap nights in dry season, 1998), 0.26 (n = 3039 trap nights for wet season, 1999), 0.15 (n = 5312 trap nights for dry season 2000) compared with 0.21 (n = 11,010 trap nights for dry season, 2002 and wet season, 2003) here (Caro, 2001, 2002). In this study, overall trapping success was low, at an average of only 6.6% throughout the study period and averaged across all habitat types. Previous success in this area was similar: 8.2% and 1.4% for two dry seasons and 3.6% for a wet season. (Caro, 2001, 2002). Interestingly, trapping success in the present study did not change markedly across seasons in line with earlier studies in the same area (Caro, 2001, 2002). In other miombo sites small mammal abundance often changes seasonally, the classic pattern being high abundance in mid-dry season, a decline in late dry season, an increase in early wet season, and a decline again in late wet season (e.g. Taylor & Green, 1976; Happold & Happold, 1990, 1991). Absence of strong seasonal changes may be a consequence of relatively low rainfall during the wet season 2002–2003.

There were few differences in species richness between habitats. In contrast, the relative abundance of small mammals showed far more marked variation across habitats, with many more individuals being caught in cultivated landscapes and in open woodland. This effect was principally because of *M. natalensis* and to a lesser extent *A. chrysophilus* being caught in large numbers in old maize and millet fields as well as open woodland areas. *Mastomys* can attain very high densities in agricultural landscapes (Christensen, 1996) and periodic population explosions are still a common feature in East Africa today (Liers, Verhagen & Verheyen, 1994; Liers *et al.*, 1997). Community differences in the relative abundance of small mammals in this miombo habitat clearly hinge on particular numerous species, here murids such as *A. chrysophilus* and *M. natalensis*, and *Crocidura* species.

When more detailed environmental measures were considered, our main finding was that small mammals definitely preferred taller vegetation as measured by species richness and relative abundance. Before turning to each

species individually, it is instructive to note that other small mammal studies in miombo habitat often vary dramatically in how they report habitat preferences. Here, we make particular reference to Vesey-Fitzgerald's (1966) study because it was also conducted in the Rukwa Valley and because of its detailed natural history. First, our microhabitat measures showed that *S. campestris* tended to inhabit leafy and tree-covered environments. In contrast, the gross habitat measure showed a (nonsignificant) preponderance in floodplain; Vesey-Fitzgerald (1966) characterized this species as having broad habitat requirements. *Dendromus mystacalis* Heuglin, 1863, the climbing mouse, has been recorded as living in grassland (Vesey-Fitzgerald, 1966) but we caught too few to make a valid comparison. *Steatomys pratensis* Peters, 1846 is characterized as living in riverine or cultivated habitats (Vesey-Fitzgerald, 1966; Linzey & Kesner, 1997b) and our composite habitat measure confirmed this indicating a (nonsignificant) preference for open riverine habitat. Vesey-Fitzgerald (1966) reported *T. boehmi* as living in herbaceous cover and *T. leucogaster* as living in woodlands characterized by sandy soils (see also Linzey & Kesner, 1997b). In line with this, microhabitat measures showed that *T. leucogaster* eschewed herb and tree cover whereas the composite measure suggests a higher abundance in cultivated habitats. *Acomys spinossisimus* Peters, 1852 has been reported as occupying rocky and woodland habitats (Vesey-Fitzgerald, 1966; Linzey & Kesner, 1997b) but we caught too few to verify or refute this.

Aethomys chrysophilus and *Aethomys kaiseri* Noack, 1887 have been reported as inhabiting mopane woodland, rocky terrain, bush and savannah (Delany, 1971; Gliwicz, 1987; Happold & Happold, 1987; Linzey & Kesner, 1997b) and an absence of significant association with anything but cultivation in this study supports the idea that *A. chrysophilus* is a habitat generalist. In addition, this species was captured in most habitats based on our composite measure. We caught very few *A. niloticus* but it is known to inhabit woodland (Senzota, 1982) and grassland (Vesey-Fitzgerald, 1966) habitats. *Grammomys dolichurus* Smuts, 1832 is arboreal and it was principally captured in woodland (Table 2). Surprisingly, we found no association with tree or shrub cover microenvironments. *Lemniscomys rosalia* reportedly lives in heavy grass cover (Linzey & Kesner, 1997b) but we found no association with such a habitat; indeed the composite measure showed it living in a wide variety of gross habitat types. *Lemniscomys striatus* has been recorded as living near streams and living around

thick grassy tussocks (Vesey-Fitzgerald, 1966) but it is also noted in grassland (Delany, 1971). Our results, which show a negative association with distance to water, and a tendency towards higher abundance in open woodland shed no further light on these divergent views.

Mastomys natalensis was found predominantly in cultivated landscapes and in large numbers as reported in a number of other studies (e.g. Christensen, 1996; Liers *et al.*, 1997). We found that *M. musculoides* numbers were high in woodland habitats but were negatively associated with shrub cover; although data on habitat preferences of this species in miombo habitat from other studies are scarce. *M. triton* has been found in bushland, savannah (Delany, 1971), dense vegetation (Vesey-Fitzgerald, 1966), and a range of habitats (Happold & Happold, 1987). We found it living in (nonsignificantly) high numbers in open woodland and our lack of significant microhabitat associations from this study support the idea that it is a generalist. We expected to find *Pelomys fallax* Peters, 1852 associated with water as reported elsewhere (Vesey-Fitzgerald, 1966) but the very small number caught prevented detailed analysis. *Graphiurus murinus* is arboreal (Delany, 1971) and we found it associated with leaf and tree cover, and with closed woodland. Habitat requirements for *Petrodromus tetradactylus* Peters, 1846 are poorly known and we caught only one in our study; however, this species is apparently largely confined to lowland and montane forest, and dense woodland, exactly the habitat in which we trapped this species.

In summary, quantitative data on vegetation types recorded in this study shed additional light on habitat preferences of small mammals living in miombo–mopane woodland. Different results from measurements taken at quite different scales suggest that different scale-dependent processes are operating to determine both the presence–absence of a species and its local abundance (see Levins, 1992). We suspect that gross habitat types are more important in determining absolute suitability (presence–absence) whilst local microhabitat measures better determine local abundance. More generally, findings using composite habitat measures and microhabitat measures were often conflicting pointing to the importance of taking measurements at both a fine and coarse scale.

Acknowledgements

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