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Habitat Preferences of Small Mammals on Mount Elgon, Uganda

by

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Abstract: A live-trapping programme for censusing small mammals was conducted on Mount Elgon, Uganda. Trapping in 4 different habitats revealed the presence of thirteen small mammal species during 3200 trap nights. Eight rodent species and five insectivore species were represented, and one of the latter, *Crocidura allex,* was a new shrew record for Uganda. The 4 most abundant rodent species were *Praomys jacksoni, Lophuromys flavopunctatus, Dendromus mesomelas* and *Rhabdomys pumilio,* and the most abundant shrew species was *Crocidura fumosa.* Species density and diversity varied considerably between the macrohabitats studied. Greater species richness was demonstrated at the most disturbed sites, though individual abundance was found to be higher in the least disturbed site (forest). Fifteen habitat variables measured around the traps were used to determine the microhabitat preferences of the four most common rodent species. *P. jacksoni* and *L. flavopunctatus* were habitat generalists and were encountered within all the microhabitats, although they were more common in fallen logs or dense litter cover. *D. mesomelas* was also considered as a generalist as it was encountered in three microhabitats but was less associated with litter depth and fallen logs and showed more preferences to open, herbaceous areas than *P. jacksoni* and *L. flavopunctatus. R. pumilio* was found most in microhabitats characterised by dense herbaceous growth, avoided the dry soil of burnt bushland. The observed differences in microhabitat use generally confirmed the already available information for the small mammals of East Africa.

Résumé: Un programme de piègeage a été conduit sur le Mont Elgon, en Ouganda, Afrique de l'est pour recenser les populations des petits mammifères. Après 3200 nuits de piégeage, ce programme a révélé la presence de treize espèces de petits mammifères dans quatre habitats différents. Huit espèces de rongeurs et cinq espèces d'insectivores étaient capturées, la musaraigne *Crocidura allex* pour la première fois en Ouganda. Parmi les espèces les plus fréquement capturées figurent quatre rongeurs, *Praomys jacksoni, Lophuromys flavopunctatus, Dendromus mesomelas* et *Rhabdomys pumilio* ainsi que la musaraigne *Crocidura fumosa.* La densité ainsi que la diversité des espèces variaient considérablement selon les macrohabitats étudiés. Une plus grande richesse spécifique a été constatée dans des endroits très perturbés, relativement aux endroits moins perturbés, tels que la forêt où l'abondance des petits mammiferes était supérieure. Quinze variables caractérisant chaque habitat piégé ont été mesurées pour déterminer les préférences de microhabitat des quatre espèces de rongeurs les plus fréquentes. *P. jacksoni* et *L. flavopunctatus* apparaissent comme étant des généralistes présents dans tous les microhabitats. Néanmoins, ces espèces montrent une préference pour les branches tombées ou encore la litière epaisse. *D. mesomelas* rentre dans la même catégorie de généralistes, car il a été observé dans trois microhabitats différents, mais, contrairement aux deux espèces précédentes, il préfère les espaces largement ouverts et herbacés. Le rongeur *R. pumilio* a tendance à fréquenter les zones où la vegétation herbacées était dense et evite les sites avec un sol sec comme celui de la brousse détruite par le feu. Les différences observées dans l'utilisation des microhabitats, ont, en règle générale, confirmés les informations déjà disponible sur les petits mammifères en Afrique de l'est.

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1. Introduction

In recent years increasing numbers of studies on small mammal populations have appeared with regard to home range, behaviour or habitat selection. The latter will be the central focus in this study.

Habitat is a spatial concept for describing the typical environment of a particular organism, population, community or even ecosystem. By studying how such ecosystems, communities and populations change over time, important insights are gained into why changes occurred, together with a good basis for predicting the likely nature of future changes. Habitat selection undoubtedly plays a major part in determining the nature and the outcome of interspecific competition for many small mammals, in which some species may have microhabitats which are complementary (i.e. variables limiting one species complement those that limit other species). Many studies have been undertaken on segregation of coexisting rodent species into structurally distinct microhabitats. Several habitat variables such as foliage height diversity, vegetation density or soil structure, significantly influence species distributions both between and within habitats (Rosenzweig et al. 1969).

The distribution and abundance of small mammals may, likewise, be affected by human disturbance such as deforestation, burning or by grazing and trampling of cattle. Delany (1971) observed that any kind of habitat modification of the primary forest has a serious effect on the species composition, diversity and total biomass of small mammals. In addition, grazing and trampling by cattle on Mt. Elgon have shown that the height of herbaceous and shrub vegetation decreases, causing higher exposure of the soil surface (Reed 1997). Extensive changes in any kind of habitat are presumed to be responsible for the consequent changes in small mammal populations and in order to understand better how resources are partitioned among coexisting species, trapping success in relation to microhabitat features are valuable to understand the use of resources such as food items.

So far, limited work on the small mammal fauna of the upper montane forest zone has been conducted and concentrated upon macro/microhabitat requirements. The small mammal fauna of Mt. Elgon has suffered from intensive disturbances of habitat modifications, such as grazing, removement of livestock or deforestation. Furthermore, no surveys have yet concentrated upon insectivore composition within the upper montane forest of Mount Elgon National Park, hence assessed to what extent habitat-induced modifications affect the insectivore species richness and distribution. This study aims to determine macro and microhabitat differences among the small mammal species, to determine which microhabitat variables significantly influence segregation of co-existing small mammals and specifically to test the hypothesis that the small mammals prefer the same microhabitat. Hence, the existing list of small mammal species on Mount Elgon may be extended, with particular emphasis on insectivores as this group has not yet been regarded as a focus of conservation.

2. Methods

The small mammal fauna was surveyed by an opportunistic live-trapping program. Trap lines cover a wide variety of habitats at once and therefore detect movement between adjacent habitats (Gurnell 1982). Traps were set out as transect lines at the four different sites. Two trap lines, each of 500 m, were set at each site, making a total of 8 transect lines. One line was laid out on either side of the path. In this way many different areas of the particular habitat

could be surveyed. The lines were made up of 25 trap sites along the transect, approximately 20 m intervals. Two large (9 x 7.5 x 23 cm) aluminium Sherman traps were positioned at each trap site, one either side of the transect, at least 6m apart and in positions likely to maximise small mammal captures (i.e. alongside fallen logs or tree roots, in herbaceous cover, in deep leaf litter). Two different baits were used in order to catch the full range of rodent and shrew species. Odd numbered traps were baited with dried fish, while even numbered traps were baited with peanut butter. Each trap was placed in a transparent polythene bag to afford protection against rain and to provide some insulation.

All 100 traps were put in place one day, left closed overnight and were opened for five days and nights, closed for a night and then reopened for further three nights (Gurnell 1982). This gave a total of eight nights of trapping per 1000 m transect. The first night of trap closure allowed shy animals to adjust while the closure at day five prevented individuals becoming trap happy. The trap lines were checked twice a day, at dawn between 0700 h-1100h and at dusk between 1600 h-1800 h. With 100 traps per study site and a trapping period of 8 nights, a total of 800 trap nights per 1000m transect was attained, giving an overall total of 3200 trap nights.

3. Study area

The study area was located near the Piswa patrol hut on the north-western side of the mountain within several kilometres of the Bennet grasslands, an area within the forest zone which has been maintained as a deflected climax by heavy grazing. The study site varied between 2800-2950 m in altitude in an approximately 5 km radius around the Piswa Patrol camp. As there are no completely undisturbed areas of forest, four main types of habitats were identified; forest, bushland, grassland and bushland which has been burnt by poachers in February 1997 but showing signs of vegetation recovery. A random sampling procedure was followed to select study sites within each habitat type. At each study site recordings of altitude were taken by using an altimeter, the aspect by using a compass and co-ordinates with help of a Global Positioning System (GPS). Access to study sites can only be gained by foot. Trapping was carried out between the end of June until end of August, a period of 6 weeks.

Macrohabitat description

Four different macrohabitat types were identified, each with different levels of modification, thereby allowing a comparison of species composition and abundance within these habitats. **Forest**, referred to an area in which trees e.g. *Carduus kikuyorum, Pennisetum clandestinum* (Reed 1997) over 20 m in height form a closed canopy, or to a more open area, resulted from modifications such as grazing, forestation or movement of livestock. **Burnt bushland** showed patches which had almost recovered and provided new plant communities, though fire damage was still evident. Other patches were yet marked badly by the burn, showing much bare soil and scars on the ground as well as burns on tree trunks. **Bushland** was dominated by woody herbs and shrub species. A tree canopy was absent or below 5% cover in most areas. A sparse understorey of forbs, pteridophytes and grasses existed beneath the shrub layer. Bushland had been partly emptied by cattle, showing many open grassy patches throughout the habitat. Where grazing was not possible, shrubs formed a closed canopy between 1-2 m above the ground. **Grassland** was dominated by herbaceous species under 10 cm height. Only occasional shrub species and herbs over 10 cm were found, occurring with increasing frequency towards the forest edge. These grasslands were heavily grazed by donkeys, cattle and goats.

Microhabitat description

In order to provide an indication of the relative amounts of food available in these macrohabitats, more detailed habitat data were collected at trap sites which had three or more captures. Captures which only occurred once or twice were excluded as a small mammal could have been captured while travelling through that particular habitat to reach a more suitable habitat. Four criteria guided selection of the habitat variables for measurements (Dueser & Shugart 1978); each variable should provide a measure of the structure of the environment which is either known or reasonably suspected to influence the distribution and abundance of small mammals; each variable should be quickly and precisely measurable with non-destructive sampling procedures; each variable should describe the environment in the immediate vicinity of the capture site, so that subtle differences among microhabitats which appeared to be grossly similar could be detected. Fifteen habitat variables were measured around each trap in all four habitats to measure floristic composition of six strata levels of the habitat: overstorey, understorey, shrub level, herbaceous level, forest floor and leaf litter level (Table 2) (Dueser & Shugart 1978).

4. Results

Capture records, spatial overlap and species diversity

A total of 13 species of small mammals were captured. This included 5 species of shrews belonging to the subfamily Soricidae, of which *Crocidura allex* represents the first record for Uganda and 8 species of rodents, of which 2 families were represented, the Muridae and the Cricetidae.

With 3200 trap nights, the capture rate was 19.7 animals per hundred trap nights, with an average number of 1.9 captures per successful trap site. The 607 captures of rodent species included 52% *Praomys jacksoni*, 27% *Lophuromys flavopunctatus*, 12% *Dendromus mesomelas*, 5% *Rhabdomys pumilio*, 4% *P (Hylomyscus) denniae*, 0.5% *Arvicanthus niloticus*, 0.3% *Oenomys hypoxanthus*, 0.1% *Mus triton*. The majority of rodent captures were at multiple-species sites (65%), showing a clear tendency of rodents to share their space with other species (Table 1). More than one rodent species was often caught at a trap site. For the most frequently captured rodent species, a 20% temporal overlap of the overall capture sites occurred between *P. jacksoni* and *L. flavopunctatus*. 45% of the *P. jacksoni* capture sites were found to overlap with the capture sites of *L. flavopunctatus* and 70% of *L. flavopunctatus* were caught at the same trap sites as *P. jacksoni*. Other overlaps occurred between *P. jacksoni* and *D. mesomelas* (13%, 34%), *L. flavopunctatus* and *D. mesomelas* (14%, 24%). Each pair of the 3 most common rodent species, *P. jacksoni, L. flavopunctatus* and *D. mesomelas*, were tested for association with a two-way contingency analysis of the frequency of presence and absence. All the 3 pairs showed significant association; these 3 rodent species were trapped at the same stations more frequently than expected ($\chi^2 = 12.02$, df = 1, $p < 0.01$ for *L. flavopunctatus* and *D.mesomelas*; $\chi^2 = 4.9$, df = 1, $p < 0.05$ for *L. flavopunctatus* and *P. jacksoni*; $\chi^2 = 48$, df = 1, $p < 0.01$ for *P. jacksoni* and *D. mesomelas).*

The 24 captures of shrews included 12.5% for each of *Crocidura allex* and *Crocidura turba*, 4.1% *Crocidura luna*, 62.5% *Crocidura fumosa* and 8.4% *Crocidura olivieri*. Compared to rodents, insectivore species tend to have a much weaker cohabitation with other species (62.5% at single species sites).

Table 1. Numbers of captures, individuals observed and capture sites in each habitat type for the 4 most frequently captured rodent species, together with the overall rodent capture record.

Habitat type	Captures	Individuals observed	Capture sites	Single sp-sites	Multiple spp-sites
Lophuromys flavopunctatus					
Forest	63	37	41	5	36
Burnt bush	66	32	28	4	24
Bush	30	15	14	5	9
Grass	3	2	3	1	2
Total	**162**	**86**	**86**	**15**	**71**
Praomys jacksoni					
Forest	187	149	73	37	36
Burnt bush	101	66	45	11	34
Bush	22	16	12	3	9
Grass	6	4	5	3	2
Total	**316**	**235**	**135**	**54**	**81**
Dendromus mesomelas					
Forest	0	0	0	0	0
Burnt bush	49	35	33	8	25
Bush	17	15	12	7	5
Grass	5	3	5	5	0
Total	**71**	**53**	**50**	**20**	**30**
Rhabdomys pumilio					
Forest	0	0	0	0	0
Burnt bush	0	0	0	0	0
Bush	18	8	10	1	9
Grass	12	5	6	4	2
Total	**30**	**13**	**16**	**5**	**11**
GRAND TOTALS (including the 3 other rodent species)					
Forest	250	186	114	42	72
Burnt bush	242	152	126	27	100
Bush	88	55	49	16	33
Grass	27	15	20	14	6
TOTAL	**607**	**408**	**309**	**99**	**211**

Macrohabitat selection

A different species diversity and richness was found in the all the four habitats. The highest number of rodents and shrews (i.e. 252) were trapped in forest. However, this habitat was only represented by 2 species of rodents and one species of shrew. Second highest capture rate was found in burnt bushland where 248 animals (6

species of rodents and 2 species of shrews). Ninety-nine animals in total including 5 rodent species and 3 shrew species were represented in bushland. Lastly, the lowest number of animals (i.e. 32) but including 5 species of rodents and 2 species of shrews, was encountered in the grassland macrohabitat.

For insectivores, the highest proportion of captures was represented by *C. fumosa* (62.5%) which was found among all the macrohabitats apart from forest. Forest was marked only by *C. olivieri*. The captures of *C. fumosa* and *C. luna* in bushland were proportionally higher than captures of the same species in the overall trapping record (none were caught in forest). *C. turba* occurred only in burnt bushland while *C. allex* was captured in grassland and bushland.

A chi-squared test was used to test for differences between observed and expected frequencies of rodents in different habitats. The test was only carried out for the 4 most common rodent species, *P. jacksoni, L. flavopunctatus, D. mesomelas* and *R. pumilio*. The outcome of this test showed that there is a statistically highly significant departure from homogeneity between the four habitats. There are significantly more *P. jacksoni* than other species and that *R. pumilio* is in a minority. Significantly less *L. flavopunctatus* were captured in forest and grassland than would have been expected by the null hypothesis that there were equal numbers in all the four habitats (P=0.01). The same accounts for *P. jacksoni* in burnt bushland, bush and grassland. Significantly more captures of *D. mesomelas* and *R. pumilio* occurred in the habitats than would have been expected with the same null hypothesis. Furthermore, the same test revealed significantly more captures in bushland for *L. flavopunctatus* and in forest for *P. jacksoni*.

Table 2. Descriptions and sampling techniques for 15 variables used to measure habitat composition based on methods developed by Dueser & Shugart (1978). GBH- girth at breast height

Variables	Methods
OVTRS	Mean diameter (gbh) of nearest overstorey tree (>8 m high) in quarters around trap
OVTRD	Mean distance (m) from trap to nearest overstorey tree in quarters around trap
UNTRS	Mean diameter (gbh) of nearest understorey tree (>8 m high) in quarters around trap
UNTRD	Mean distance (m) from trap to nearest understorey tree in quarters around trap
WOSTD (0 m)	Live woody stem count at ground level (0m) within 2 m^2 circle centred on trap
WOSTD (0.5 m)	Live woody stem count at 0.5 m height within 2 m^2 circle centred on trap
WOSTD (1.0 m)	Live woody stem count at 1.0 m height within 2 m^2 circle centred on trap
HESTD (0 m)	Live herbaceous stem count at ground level (0 m) within 2 m^2 circle centred on trap
HESTD (0.5 m)	Live herbaceous stem count at 0.5 m height within 2 m^2 circle centred around trap
HESTD (1 m)	Live herbaceous stem count at 1 m height within 2m^2 circle centred on trap
FALOGS	Mean diameter (cm) of nearest fallen log (diameter > 7.5 cm) in quarters around trap
FALOGD	Mean distance (m) from trap to nearest fallen log in quarters around trap
LECO %	Estimation of the percentage of bare ground within 2m radius circle of trap
LEDE	Mean depth (cm) of litter layer at 4 perpendicular points around trap
LIASTD	Number of liana stems within 3 m radius of trap

The same hypothesis that the shrew species are distributed equally in the four habitats is rejected (df=12, $p < 0.01$). The numbers of captures of *C. allex* exceed expectations in the grassland but are less than expected in the bushland. *C. fumosa* was taken more frequently than expected in bushland but less frequently than expected in grassland and burnt bushland. *C. turba, C. luna* and *C. olivieri* were each caught in only one habitat and this more frequently than expected. However, although the shrews were not caught in sufficient numbers, it can only be assumed that these species are restricted to certain habitats.

Microhabitat selection

To determine the habitat variables that distinguish between the microhabitats of different species, the trap sites of the 4 most commonly caught rodent species were compared (Table 3). Kruskal-Wallis test was used to distinguish between the medians of samples for obvious relationships with structural variables. Six variables were found to distinguish between microhabitats of different species: overstorey tree dispersion and size, fallen log dispersion and size, leaf litter depth and cover. The null hypothesis that small mammals show similar microhabitat preferences can therefore be rejected for any particular variable. However, the rejection of the null hypothesis does not imply that all four sample means are different from one another nor does it reveal how many differences there are and where they are located among the species. As there are unequal numbers of data in each sample, the Dunn test (1964 as cited by Zar 1997) was used. If the four species are compared with each other (Table 4), it is clear that *L. flavopunctatus* and *P. jacksoni* do not differ in any of the six microhabitat variables, which means that they probably favour the same habitat. The same applies to *D. mesomelas* and *R. pumilio*, only with respect to two microhabitat variables, which also suggests that those two species may prefer the same microhabitat. There is clearly highly statistically significant departure from homogeneity between the other pairs of rodent species, especially between *P. jacksoni vs. R. pumilio* as well as *L. flavopunctatus vs. R. pumilio.*

Table 3. Sample estimates of the species means (x) and standard deviations (s) for each of the 15 habitat variables observed for each of the 4 most common rodent species. ★: significantly different.

Microhabitat variables	*Praomys jacksoni* (n=49) x ± *s*	*Lophuromys flavopunctatus* (n=38) x ± s	*Dendromus mesomelas* (n=11) x ± s	*Rhabdomys pumilio* (n=6) x ± s
★ OVTRS (m)	5.64 ± 5.39	5.55 ± 4.78	5.6 ± 4.04	1 ± 1.56
★ OVTRD (cm)	139.09 ± 90.42	138.11 ± 83.32	83.76 ± 76.36	56.67 ± 93.31
UNTRD (m)	2.87 ± 2.9	2.66 ± 2.52	2.42 ± 0.89	5.35 ± 5.21
UNTRS (cm)	31.97 ± 18.39	30.76 ± 18.5	32.36 ± 11.67	28.5 ± 18.02
WOSTD (0 m)	14.16 ± 12.64	14.34 ± 13.62	7.09 ± 6.3	10.5 ± 8.64
WOSTD (0.5 m)	9.04 ± 6.22	9.1 ± 7.45	6.82 ± 6.27	10.5 ± 8.64
WOSTD (1.0 m)	4.35 ± 4.23	3.84 ± 4.02	5.45 ± 4.13	6.17 ± 6.62
HESTD (0 m)	113 ± 67.91	104.1 ± 65.55	133.91 ± 73.6	123.83 ± 114.14
HESTD (0.5 m)	62.84 ± 51.1	55.46 ± 47.56	79.91 ± 52.49	47 ± 40.03
HESTD (1.0 m)	6.47 ± 8.96	6.58 ± 8.62	0.64 ± 1.29	0.83 ± 0.75
★ FALOGD (m)	0.53 ± 0.9	0.7 ± 1.35	0.06 ± 0.14	0.05 ± 0.12
★ FALOGS (cm)	15 ± 16.6	16.6 ± 18.45	4.09 ± 9.17	1.67 ± 4.08
★ LEDE (cm)	55.26 ± 78.47	65.52 ± 81.45	10.27 ± 34.07	0 ± 0
★ LECO %	1.75 ± 3.62	1.29 ± 1.86	0.38 ± 1.27	0 ± 0
LIADEN	3.18 ± 3.88	3.44 ± 3.89	2.55 ± 2.16	0 ± 0

Table 4. Nonparametric multiple comparisons, using the Dunn test for the six significant microhabitat variables (★; Table 3) against each species examined; * < 0.05, ** < 0.01, *** < 0.005.

	Species	*P. jacksoni*	*L. flavopunctatus*	*D. mesomelas*	*R. pumilio*
OVTRD (cm)	*P. jacksoni*	-			
	L. flavopunctatus		-		
	D. mesomelas	**		-	
	R. pumilio	**	**	**	-
		P. jacksoni	*L. flavopunctatus*	*D. mesomelas*	*R. pumilio*
	P. jacksoni	-			
OVTRS (m)	*L. flavopunctatus*		-		
	D. mesomelas	*	**	-	
	R. pumilio	***	***		-
		P. jacksoni	*L. flavopunctatus*	*D. mesomelas*	*R. pumilio*
	P. jacksoni	-			
LEDE (cm)	*L. flavopunctatus*		-		
	D. mesomelas	**	*	-	
	R. pumilio	***	***	*	-
		P. jacksoni	*L. flavopunctatus*	*D. mesomelas*	*R. pumilio*
	P. jacksoni	-			
LECO %	*L. flavopunctatus*		-		
	D. mesomelas	*	*	-	
	R. pumilio	***	***		-
		P. jacksoni	*L. flavopunctatus*	*D. mesomelas*	*R. pumilio*
	P. jacksoni	-			
FALOGD (m)	*L. flavopunctatus*		-		
	D. mesomelas	**	**	-	
	R. pumilio	**	**		-
	Species	*P. jacksoni*	*L. flavopunctatus*	*D. mesomelas*	*R. pumilio*
	P. jacksoni	-			
FALOGS (cm)	*L. flavopunctatus*		-		
	D. mesomelas	*	*	-	
	R. pumilio	**	**		-

As the data collected on shrews was not sufficient to determine significant differences in habitat preferences and niche partitioning, it was impossible to classify them ecologically as belonging to particular vegetation zones. Only a brief description of microhabitat characteristics of sites inhabited by the five shrew species are given in the discussion.

A separate multivariate statistical procedure, principal component analysis (PCA), was carried out on the data from 60 capture sites for the four habitats. Only capture sites which had three or more captures were considered for this procedure. Principal component analysis was carried out for each of the fifteen microhabitat variables in an

attempt to summarise descriptively the main sources of variation between each habitat. Eigenvalues for each component represent the relative importance of the axis by accounting for the variances in the data (Table 5). The first component (PCA I) explains about 21% of the total variation in the sample and is overwhelmingly the main source of variation among habitat variables. The second component (PCA II) explains about 14% of the total variation. Eigenvectors represent the weighting of each microhabitat variable. The habitat variables with the highest negative coefficients for the first axis (PCA I) are litter depth, litter cover, fallen log dispersion and size, while high positive values occur with understorey tree size (Table 5). The important positive factors in PC II were woody stem density at ground level and 0.5 metres of the ground and the negative factors were herb stems at 0 & 0.5 m.

The positions of individual trapping stations with respect to PC I and PC II revealed four microhabitats. Forest (microhabitat 1) forms almost a completely isolated group with high negative values on the first axis (PCA I) and high positive values on the second axis (PCA II). The vegetation of this habitat can be seen as most heterogeneous of all the microhabitats. A slight overlap was found between burnt bushland and bushland. Woody stems were mostly found at the ridge where burnt bushland and bushland overlapped. Considerable overlap exists between bushland and grassland. The vegetation of these two habitats seems to be most homogeneous and can therefore be categorised as a single microhabitat.

Table 5. First two principal components for microhabitat data showing eigenvalues and eigenvectors for each component as well as their individual variation.

	Eigenvalues (unscaled)	
	PCI	**PCII**
Variate	3.214	2.16
	Eigenvectors	
OVTRD (cm)	0.0165	-0.2969
OVTRS (m)	-0.2813	-0.2199
UNTRD (m)	0.2022	0.2425
UNTRS (cm)	0.2859	0.1800
WOSTD (0 m)	-0.2032	0.4946
WOSTD (0.5 m)	-0.1077	0.4200
WOSTD (1.0 m)	0.1912	0.1744
HESTD (0 m)	0.0649	-0.3468
HESTD (0.5 m)	0.1437	-0.3611
HESTD (1.0 m)	-0.1649	-0.0272
LEDE (cm)	-0.3695	-0.1390
LECO %	-0.4212	-0.1026
FALOGS (cm)	-0.3903	0.1857
FALOGD (m)	-0.3600	0.0351
LIADEN	-0.2462	-0.0625
Variance (%)	21.42	14.4

5. Discussion

Given that the species richness of the present study (13) is similar to that of previous studies (Delany 1971, Davenport 1996 and Cameron 1997), and also that trapping protocols and periods were similar and that each study resulted in new records, it is suggested that the evaluation of small mammal species diversity on Mount Elgon has still not been finalised. This is confirmed by the fact that the present survey revealed a further new record of an insectivore species, *Crocidura allex* which has not been recorded previously on Mount Elgon nor in Uganda. This species was encountered only in bushland and grassland, hence if it is dependent more upon cultivated habitats, its absence from earlier records might be explained by the fact that former cultivation of Mount Elgon has been reduced as a result of the lower population within the park. Moreover, in line with the findings of many other studies (Delany 1971, Kasenene 1984 and Project Elgon Report 1997), the present study found in general a higher diversity, but not necessarily a higher proportion, of rodents as well as shrew species in disturbed habitats than in undisturbed ones. Despite the fact that cultivation and grazing significantly alter plant communities in the upper montane forest and reduce tree regeneration, the species richness of plant communities and small mammals increases (Project Elgon Report 1997).

Small mammal macrohabitat use

The results of this study indicate that different macrohabitats on Mount Elgon support unequal densities and diversities of rodents and shrews. The Chi-square test for homogeneity shows highly significant differences in small mammal composition between the four different macrohabitats ($p < 0.01$). The small mammals seem to allocate their time within these habitats according to the measured structural properties of the vegetation on these macrohabitats.

Examination of the rodent distribution in the four macrohabitats revealed that *Praomys jacksoni*, *Lophuromys flavopunctatus* and *Dendromus mesomelas* had the most generalised distribution, of which the two former were encountered in all habitats and the latter only in three macrohabitats, whilst the remainder were much more restricted in their habitat use. The findings of earlier studies (Delany 1971, Davenport et al. 1996 and Cameron 1997) have shown similar patterns of generalisation of *P. jacksoni* and *L. flavopunctatus* as being widespread throughout different habitats, especially moist forest areas. *D. mesomelas*, found in three out of four habitats in the present study, showed a higher incidence (12%) of captures than the previous study (1%). The fact that these species have only recently been recorded on Mt. Elgon (Cameron, 1997) shows that they have successfully radiated into nearly all the niches on Mt. Elgon. The overall high abundance of burnt bushland, almost as much as forest, and the high species richness may be due to the fact that these new regenerating plant communities provide plentiful food sources. On the other hand, *Rhabdomys pumilio*, being the fourth most abundant species, avoids bare areas such as those denuded by burning (Rowe-Rowe & Lowry 1982 as cited in Shore et al.1991). In fact, the present study recorded *R. pumilio* only in bushland and grassland, hence excluding the drier conditions and soil structure of burnt bushland.

Examination of the rodent distribution and abundance was limited mostly to the four species. Though the sample sizes are small for the remaining rodent species encountered, brief conclusions may be drawn. The presence of *P. (Hylomyscus) denniae, Oenomys*

hypoxanthus and *Arvicanthus niloticus* only in burnt bushland, apart form the latter of which one record was from bushland, and *Mus triton* only in grassland, are not entirely in accord to earlier studies (Kingdon 1974, Davenport et al. 1996 and Cameron 1997). However, as already mentioned, the occurrence of high species richness in burnt bushland due to the high productivity of regenerating plant communities, may explain the apparent change in distribution of these species. It is also relevant that burnt bushland was in close proximity to forest habitat, hence foraging may have occurred whilst travelling through this highly suitable and rich macrohabitat.

In the course of this study, five species of shrews were caught within four different habitats. The information presented here provide the first quantitative data on relative abundance and habitat selection of these rare populations of the montane forest zone. Because the survey has mainly captured rodent species, the 24 shrews that were collected constitute only 3.8% of the total captures of small mammals and is therefore not a reliable index of abundance or distribution. Furthermore, as all the specimens were identified by Robert Kityo at Makerere University where they are still held, no further morphological data on dentition and skulls was given apart from the species name. Bearing in mind that few attempts have been made to survey the insectivore fauna on Mount Elgon, and very little is known of the general biology and ecology of Ugandan shrews, direct comparison of the present survey results will be difficult as little literature is available on the Ugandan insectivore fauna.

C. olivieri is the largest species of shrew among the five species encountered. It was found in and around vegetation types such as sparse bushes, dense herb layers, dense shrubs and sparse litter cover. It was also found close to paths and forest edges and where signs of grazing by cattle were noticed. *C. luna*, although only captured once, was found in a heavily grazed vegetation area with only a few heather bushes and no litter cover at all. Capture sites of *C. turba* were identified as such with dense to average herb layers and woody stems, light to sparse litter cover and some were located close to the forest edge. *C. fumosa* and *C. allex* were both found in vegetation patches with dense herb layers and shrubs, sparse bushes and litter cover, close to the forest and where signs of grazing were observed.

Small mammal microhabitat use

The results of this study showed that four forest-floor rodents, *P. jacksoni, L. flavopunctatus, D. mesomelas* and *R. pumilio* exploit microhabitats which differ significantly in structure within a certain macrohabitat. The fifteen microhabitat variables permitted a detailed analysis of habitat structure, of which six habitat variables were identified to differentiate between small mammal microhabitats. PCA confirmed the differences detected by the habitat assessment and revealed three distinct microhabitat groups. Microhabitat 1, coinciding with forest, was characterised by litter cover and depth, fallen log dispersion and size as well as woody stem density and average herb stem density. Only 2 rodent species, *P. jacksoni* and *L. flavopunctatus*, occurred in this habitat. The choice of such dense and rich areas may be related to a high primary productivity or the need for good protection. The Dunn test did not reveal any difference in preferred microhabitat variables between these two species. Furthermore there was a considerable temporal overlap found between *P. jacksoni* and *L. flavopunctatus*, which is confirmed by the Chi-square test showing that this pair of species was trapped at the same trap stations more often than expected.

The lack of captures of any other rodent species in this microhabitat may be due to inter/intraspecific competition. Such competition for resources has been invoked as an explanation for size-structured communities since species of similar size may exclude one another (Adler 1994). The present study showed an overall higher abundance of *P. jacksoni* than *L. flavopunctatus* in forest which may be interpreted by the fact that interspecific competition of two similar-sized species may be greater. Although it is probable that the intensity of competition between this pair of species diminishes by temporal partitioning since *P. jacksoni* is generally believed to be mainly nocturnal. The absence of the other two species in forest, may in turn result from intracompetitive interactions since the larger ones (in this case *P. jacksoni* and *L. flavopunctatus*) could exclude the smaller ones (*D. mesomelas* and *R. pumilio*) in the overlap habitat, though there is currently no evidence for this. The second microhabitat, burnt bushland, is mainly associated with microhabitat variables such as herb stems at ground level and at 0.5 m, average understorey tree dispersion and size. In fact, the microhabitat variables of herb stem density at all levels were mainly predominated by *D. mesomelas* (Table 3). Similar microhabitat use by this species is reported in other studies (Kingdon 1974, Cameron 1997). Although *P. jacksoni* and *L. flavopunctatus* showed once more a high abundance in this microhabitat, they were much less related to herb stems than *D. mesomelas* but therefore more to woody stems (Table 3). Finally, microhabitat 3, being bushland and grassland, had the least abundance among the three microhabitats and according to the eigenvectors of PCA (Table 5), this microhabitat was mainly related to understorey tree dispersion and size and to a smaller extent to herb and woody stem density. *R. pumilio* was only found in this microhabitat which makes it in some ways complementary to the microhabitats of the other three examined rodent species. *R. pumilio* is conspicuously different from *P. jacksoni* and *L. flavopunctatus* in all the six examined microhabitat variables ($p < 0.005$) (Table 4). *D. mesomelas* was found to differ only in two variables from *R. pumilio* (Table 4), hence both species can be assumed to have similar microhabitat use.

Additionally, Dueser & Shugart (1978) observed that two species of dissimilar appearance, body size and general ecology, were most similar qualitatively in microhabitat configuration and overlap. In practical terms, this means that competition between two species of dissimilar appearance is less intense than between those of similar appearance. Although there is clear evidence of partitioning of microhabitats in the present study, the results are only consistent to a degree with this observation. For instance, *P. jacksoni* and *L. flavopunctatus* were the two most similar species in appearance, size and general ecology but were also the most similar ones in qualitative microhabitat configuration as well as niche overlap. In this case, the assumption that competition between similar-sized species is greater (Adler 1994) may be considered. Conversely, two dissimilar species in terms of appearance, size and ecology, *P. jacksoni* and *D. mesomelas*, experienced to a certain degree similar microhabitat configuration and niche overlap. The same would account for *L. flavopunctatus* and *D. mesomelas*. Differences in body size are thought to be the main mechanisms to allow coexistence of dissimilar species (Price 1978). Furthermore, the results reported here support the hypothesis that small mammal distribution is correlated to vegetation type (Rosenzweig et al.1975 as cited in Fa 1992) and that resource use differences exist between co-existing species (Brown et al. 1973). Hence, this agreement suggests that inter/intraspecific competition for foraging microhabitats may be important in structuring the small mammal fauna on Mt. Elgon.

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