
Diversity of rodents and shrews along an elevational gradient in Bwindi Impenetrable National Park, south-western Uganda

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Abstract

Small mammal species diversity in the major vegetation zones of Bwindi Impenetrable National Park is discussed in relation to altitude. Species richness of the small mammals was found to decrease with an increase in altitude. The main factors accounting for the observed diversity are the wide altitudinal variation and a complex array of vegetation types. Sixty-seven species of rodents and shrews were found to exist in the Park; 47 of which were rodents and 20 shrews. Of these, 26 species are new to the Bwindi Park list. Three species have probably not been described before. The study found 10 species of small mammals to be Albertine Rift endemics. Three genera are recorded in Uganda for the first time: *Rwenzorisorex*, *Suncus* and *Paracrociodura*. Five species are new records for East Africa. These are *Crociodura stenocephala*, *Lophuromys rahmi*, *L. medicaudatus*, *Paracrociodura maxima* and *Hylomyscus aeta*. Because of the high endemism of plants, butterflies, birds and now of small mammal species, Bwindi forest is a unique biodiversity hotspot and is among the highest conservation priorities in the Albertine Rift.

Key words: altitude, Bwindi impenetrable, endemism, rodents, shrews

Résumé

On discute de la diversité des espèces de petits mammifères dans les principales zones de végétation du Parc de la Forêt Impénétrable de Bwindi, en fonction avec

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l'altitude. On a trouvé que la richesse en espèces de petits mammifères diminuait avec l'augmentation de l'altitude. Les principaux facteurs qui expliquent la diversité observée sont la grande variation de l'altitude et un ensemble complexe de types de végétation. On a découvert que soixante-sept espèces de rongeurs et de musaraignes vivent dans le parc, dont 47 rongeurs et 20 musaraignes. Parmi eux, 26 espèces sont nouvelles sur la liste du Parc de Bwindi. Trois d'entre elles n'ont probablement jamais été décrites auparavant. L'étude a découvert que 10 espèces de petits mammifères sont endémiques au Rift Albertin. Trois genres sont rapportés pour la première fois pour l'Ouganda : *Rwenzorisorex*, *Suncus* et *Paracrociodura*. Cinq espèces sont nouvelles pour l'Afrique de l'Est : *Crociodura stenocephala*, *Lophuromys rahmi*, *L. medicaudatus*, *Paracrociodura maxima* et *Hylomyscus aeta*. Etant donné le fort endémisme de plantes, de papillons, d'oiseaux et maintenant, de petits mammifères, la forêt de Bwindi est un haut lieu unique de la biodiversité qui se range parmi les plus urgentes priorités de la conservation du Rift Albertin.

Introduction

Zonation on mountains, whereby different species of animals and plants occur at different altitudes, is a well-known ecological phenomenon. Many studies of zonation on African mountains have looked at alpine plants (Hedberg, 1951, 1969, 1986; White, 1971, 1981; Killick, 1978). Studies on animals are less numerous, although there are many species lists and casual observations from some mountain areas. Studies in the ecology of small mammals (rodents and shrews) in tropical Africa have increased in recent years (Martin, 1985). Much of the earlier work concentrated largely on the geographical

distribution of species. Delany (1972) summarized most of these studies, which formed the background for subsequent work (Cheesman, 1975; Delany & Roberts, 1978). Small terrestrial mammals in high altitude habitats have been equally well studied on some African mountains: Rwenzori (Misonne, 1963; Austin *et al.* 1992), Cameroon (Einsentraut, 1973), Kahusi (Rham & Christiaensen, 1963) and Drakensberg (Rowe-Rowe & Meester, 1982). Happold & Happold (1989) investigated the biogeographical distribution of particular species and communities on different mountains. Yalden (1988) found the small mammal fauna species richness of the Bale Mountains to increase with altitude. However on the western and eastern slopes of Rwenzori Mountains, Misonne (1963) and Austin *et al.* (1992) found the small mammal species richness to decrease with increasing altitude. Rickart *et al.* (1991) have shown high levels of variation in mammal communities along elevational gradients. Prior to this study, there was little information on the small mammal communities of Bwindi. In Bwindi Impenetrable National Park, with its location on the edge of the Albertine Rift (believed to be Pleistocene Refugia, Hamilton, 1982) and a unique altitudinal range of 1160–2607 m, such a study was deemed important. A few rodent records are mentioned by Delany (1975), however Baranga (1993) presented a preliminary list of rodents and shrews for the Park. Aleper (1995) investigated the population dynamics of rodents in three forest types, but since his work was limited to a small portion of the Park, he never gathered a comprehensive species list for Bwindi. This study was conducted to fill this gap and to collect baseline data regarding the distribution and ecology of small mammal species at different elevations in and around the Park, as well as to gain an insight into the endemism levels.

Materials and methods

The study area

The study was conducted in Bwindi Impenetrable National Park. Covering an area of 331 km², the Park occupies the highest block of the Rukiga Highlands on the Eastern edge of the Western Rift valley, and is located between latitudes 0°18' and 0°53'S, longitudes 29°35' and 29°50'E. The climate is tropical, with two rainfall peaks from March to May and September to November. The dry periods are December to January and June to August, the latter being more severe and longer

(Butynski, 1984). The favourable all year climate may provide resources necessary for small mammal survival.

The selection of study sites was performed based on altitude and the major vegetation zones of Bwindi. The major vegetation zones surveyed include: lowland forest, high altitude forest, disturbed and or degraded forest, lowland papyrus swamp, high altitude sedge swamp, bamboo forest and grassland. These are representative of the vegetation types described by Howard (1991).

We sampled 10 study sites

(i) Ruhija (RU) 2350 m. This area has experienced anthropogenic disturbances at high intensity. The area was intensively pitsawn for timber for 44 years (Howard, 1991). Common pioneer tree species such as *Polyscias fulva*, *Maesa lanceolata* and *Macaranga kilimandscharica* are an indication that the area has been impacted by human activities.

(ii) Buhoma (BU) 1500 m is a mid-altitude primary forest adjacent to degraded habitat. *Carapa grandiflora*, *Parinari excelsa* and *Ocotea kenyensis* dominate the forest. Trapping at this site was conducted in the forest (BFR) and in the surrounding degraded habitat (BDG).

(iii) Two-pond swamp (TPS) 1830 m is an open water pond bordered by a high altitude sedge swamp consisting of *Anthocleista vogelli* as the dominant tree.

(iv) Byumba (BY) 1540 m consisted of degraded and cultivation habitats outside the Park and colonizing forest inside the Park. The colonizing forest is dominated by species such as *Olea*, *Prunus africana*, *Sapium ellipticum* and *Markamiatplatycalyx*. At Byumba, trapping was done both in the forest (BYF) and in the degraded adjacent habitat (BYD).

(v) Ngoto swamp (NGS) 1280 m is a low altitude papyrus swamp.

(vi) Hamuhingo grassland (HG) 1570 m, *Hyparrhenia* sp., and a mixture of ferns and *Setaria* dominate the grassland.

(vii) Nteko forest (NTF) 1600 m is an area of private forest adjacent to the Park with a variety of microhabitats ranging from swamp forest, several phases of regenerating forest and relics of primary forest.

(viii) Bamboo zone (BA) 2503 m. *Arundinaria alpina* is the dominant vegetation interspersed with forest trees.

(ix) Mubwindi swamp (MUS) 2070 m is a sedge-rush high altitude swamp surrounded by steep densely forested slopes.

(x) Kasiresire (KA) 2060 m is a primary forest site located deep in the Park and is assumed to be virgin forest.

All together, the sites constituted an elevational range of 1280–2503 m.

Field methods

Most small mammal species are difficult to study because of their secretive habits (Delany, 1975) furthermore, the methods that have been developed are complicated by their (small mammal) small size and mainly nocturnal activity, making direct observation impracticable. In most studies, one or two of the following methods have been used for the detection of small mammals:

- 1 Non-trapping by use of trapping boards, flooding of burrows, fencing of an area followed by removal of vegetation and then hand capture of the mammals or by digging them up;
- 2 Removal trapping that involves the use of break back traps; and
- 3 Non-removal (live) trapping.

In this study, we used both live and removal trapping, as they have been widely applied on the African continent (Delany, 1964; Cheesman & Delany, 1979). This was done because one of the objectives of the study was to document small mammal species diversity at the various elevations and vegetation zones. Pucek (1969) observed that different species of small mammals are selectively trapped in relation to the type of trap and capture technique applied. He emphasized the importance of pitfall traps in sampling Soricids. Pitfalls were established in all study sites. Varying the size of the trap was found to be an effective method for trapping a broader spectrum of species (Schwan, 1986). In this study, various trap types, including the Sherman, Havarhart, Tomahawk, Museum special and Victor rat-traps were used. The last two types of trap were used in areas adjacent to the Park during an Afrotropical Biodiversity Training Programme and some of the data analysed was from this programme.

A mixture of peanut butter with rolled oats, fish, maize-meal bread and a variety of fruit leftovers were used as bait to attract a wide range of small mammal species.

Trapping was conducted along transects (trap lines) within the different habitats or vegetation types from February to December 1997. Two trap lines were set, both on the ground and at suitable locations in the bushes and trees following the method used by Kityo (1991). Trap lines were then shifted after five consecutive nights of

trapping in the same habitat. Altogether, an average of 1200 trap-nights (624–2455) were used to sample at each elevation. Traps were inspected daily, both in the morning for nocturnal species and in the evening for diurnal species.

All animals caught were identified to species level following Delany (1975), Skinner & Smithers (1990). They were sexed and weighed using appropriate Pesola spring balances. Standard measurements, reproductive status, microhabitat (e.g. near log, near stream or water and above ground), temporal activity (whether diurnal or nocturnal), trap type and bait used were recorded.

Very small Soricids were surveyed using pitfall traps, distributed in 30–50 m lines and comprised of buckets set every 5 m with barricades of polythene paper or wire mesh. The barricades were used to guide the animals into the pitfalls. The trapped animals were released or skinned, prepared as skeleton and formalin preserved. Animal tissues were taken from taxonomically problematic taxa and preserved in 95% ethanol for later molecular study. Final confirmation of the taxonomy was carried out at the Museum of Zoology, Makerere University and at the Field Museum of Natural History, Chicago.

Data analysis

The Shannon–Wiener (H') index of diversity (Shannon, 1948) was calculated for all sites sampled and evenness values were derived from it. The Shannon index increases with the number of species in a community and in theory can reach very large values. In practice, for biological communities (Krebs, 1989) H' does not exceed 5.0.

Evenness (E_1) values were derived from the expression, $E_1 = H' / \ln S$, where $\ln S$ is the natural logarithm of the number of species. Evenness values indicate how the species are distributed in a community. When the Evenness is high, the mammal fauna is more diverse and the species are equally abundant (Magurran, 1988). In order to standardize data for all sites sampled so that productivity of the habitats were compared, despite the differing trap effort, Trap Success (the number of animals caught per 100 trap nights) was calculated from the expression:

$$\text{Trap Success} = (\text{Total catch} / \text{Trap nights}) \times 100.$$

The number of species trapped per 100 trap nights (TRs) was also calculated for each site using the expression: $[\text{Species richness} / \text{Trap effort}] \times 100$. Using daily trapping

records, species accumulation rates were examined at the end of a sampling regime to estimate the extent to which further trapping would add to the species list and to facilitate comparisons of species richness between habitats for any given level of sampling effort.

All small mammal species currently known from Uganda were classified according to habitat requirements (Rosevear, 1969; Kingdon, 1971; Delany, 1975; Hutterer, 1987; Skinner & Smithers, 1990). The following ecological type categories were recognized and adopted for this study:

1 Forest-dependent species (F-species) are largely confined to closed canopy forest and would be unlikely to tolerate any form of large-scale habitat modification although they may persist in secondary forest and isolated forest fragments.

2 Forest nondependent species (f-species) are not restricted to closed canopy and may occur in forest edge, gallery forest and dense savanna woodland.

3 Non-forest (open) habitat species are characteristic of open grasslands and semi-arid environment (O), aquatic or swamp habitat (A) or occur in a wide range of habitat (W).

4 Where the species ecological category is not defined (U) has been used. Species were further classified according to whether they occurred in high altitude areas above 1800 m (H) or low altitude areas below 1800 m (L).

Results

Species richness

A total of 851 small mammals belonging to orders Rodentia and Insectivora were trapped. Sixty-seven species of rodents and shrews were confirmed to occur in Bwindi, 47 of which were rodents and 20 were shrews (Table 1). Twenty-six are new to the Park's record, with three species that are probably new to science, belonging to three genera *Suncus*, *Hybomys* and *Praomys*. Three genera *Rwenzorisorex*, *Suncus* and *Paracrocridura* were documented for Uganda for the first time. Five species were new records for East Africa and they were *Crocridura stenocephala*, *Paracrocridura maxima*, *Lophuromys rahmi*, *L. medicaudatus* and *Hylomyscus aeta*. Ten species were Albertine Rift endemics (Table 1).

Trap success was lowest at the highest elevation sampled in the Bamboo zone with 2.25%, and was highest at mid-elevation at Byumba with 14.64% (Table 1). This

Table 1 Bwindi Impenetrable National Park rodents and shrews species list. Some species are from past records, see Baranga (1993) and Aleper (1995)

Genus	Species	Habitat type	New records	Endemics
<i>Chrysochloris</i>	<i>stuhlmanni</i>	O		
<i>Crocridura</i>	<i>dolichura</i>	U	+	
<i>Crocridura</i>	<i>hildegardae</i>	O	+	
<i>Crocridura</i>	<i>luna</i>	f		
<i>Crocridura</i>	<i>maurisca</i>	O		
<i>Crocridura</i>	<i>montis</i>	UH	+	
<i>Crocridura</i>	<i>niobe</i>	U	+	
<i>Crocridura</i>	<i>olivieri</i>	W	+	
<i>Crocridura</i>	<i>stenocephala</i>	U	+	
<i>Crocridura</i>	<i>tarella</i>	U	+	
<i>Crocridura</i>	<i>turba</i>	U	+	
<i>Myosorex</i>	<i>babaulti</i>	UH	+	
<i>Myosorex</i>	<i>blarina</i>	FH		
<i>Paracrocridura</i>	<i>maxima</i>	FH	+	E
<i>Scutisorex</i>	<i>somereni</i>	FH		
<i>Suncus</i>	<i>sp.</i>	F	+	
<i>Sylvisorex</i>	<i>granti</i>	F		
<i>Sylvisorex</i>	<i>lunaris</i>	FH	+	E
<i>Sylvisorex</i>	<i>megalura</i>	O		
<i>Sylvisorex</i>	<i>vulcanorum</i>	FH	+	E
<i>Helioschiurus</i>	<i>rufobrachium</i>	U		
<i>Helioschiurus</i>	<i>rwenzorii</i>	U		
<i>Paraxerus</i>	<i>alexandri</i>	F		
<i>Paraxerus</i>	<i>boehmi</i>	f		
<i>Protoxerus</i>	<i>stangeri</i>	F		
<i>Anomalurus</i>	<i>derbianus</i>	F		
<i>Cricetomys</i>	<i>emini</i>	W		
<i>Delanymys</i>	<i>brooksi</i>	AH		E
<i>Dendromus</i>	<i>mysticalis</i>	O		
<i>Dendromus</i>	<i>sp.</i>	O		
<i>Deomys</i>	<i>ferrugineus</i>	f		
<i>Otomys</i>	<i>denti</i>	O		
<i>Otomys</i>	<i>tropicalis</i>	O	+	
<i>Tachoryctes</i>	<i>ankoliae</i>	O		
<i>Arvicanthis</i>	<i>niloticus</i>	O		
<i>Colomys</i>	<i>goslingi</i>	A		
<i>Dasymys</i>	<i>incomtus</i>	A		
<i>Grammomys</i>	<i>dolichurus</i>	W		
<i>Grammomys</i>	<i>dryas</i>	FH	+	E
<i>Hybomys</i>	<i>sp.</i>	FH	+	
<i>Hybomys</i>	<i>unvittatus</i>	f		
<i>Hylomyscus</i>	<i>aeta</i>	FH	+	
<i>Hylomyscus</i>	<i>denniae</i>	FH		
<i>Hylomyscus</i>	<i>stella</i>	F		
<i>Hylomyscus</i>	<i>vulcanorum</i>	FH	+	E
<i>Lemniscomys</i>	<i>striatus</i>	O		
<i>Lophuromys</i>	<i>flavopunctatus</i>	W		
<i>Lophuromys</i>	<i>medicaudatus</i>	FH	+	

Table 1 continued

Genus	Species	Habitat type	New records	Endemics
<i>Lophuromys</i>	<i>sikapusi</i>	O		
<i>Lophuromys</i>	<i>rahmi</i>	FH	+	E
<i>Lophuromys</i>	<i>woosnami</i>	FH		E
<i>Malacomys</i>	<i>longipes</i>	A		
<i>Mastomys</i>	<i>hildebrandti</i>	O	+	
<i>Mus</i>	<i>bufo</i>	FH		E
<i>Mus</i>	<i>gratus</i>	W	+	
<i>Mus</i>	<i>minutoides</i>	W	+	
<i>Mus</i>	<i>triton</i>	O		
<i>Oenomys</i>	<i>hypoxanthus</i>	f		
<i>Pelomys</i>	<i>hopkinsi</i>	U		
<i>Praomys</i>	<i>sp.</i>	F	+	
<i>Praomys</i>	<i>jacksoni</i>	F		
<i>Rattus</i>	<i>rattus</i>	O		
<i>Stochomys</i>	<i>longicaudatus</i>	F	+	
<i>Thamnomys</i>	<i>kempi</i>	F	+	E
<i>Thamnomys</i>	<i>venustus</i>	FH		
<i>Thryonomys</i>	<i>gregorianus</i>	O		
<i>Graphiurus</i>	<i>murinus</i>	W		

Habitat type or ecological category refers to the general habitat where a species is most likely to be found. New records refer to species that are new to the Park's rodents and shrews list or those that have not been recorded for Bwindi before this study. Endemics are species that are restricted to the Albertine Rift region.

indicates that the high altitude habitat was less productive than at intermediate elevations.

Table 2 shows that species richness was highest at the two sites Byumba and Nteko, with 22 species each. The lowest species richness was attained in the grassland and Bamboo zone with 8 species each. It is also evident from Table 2 that in all cases the rodent species were

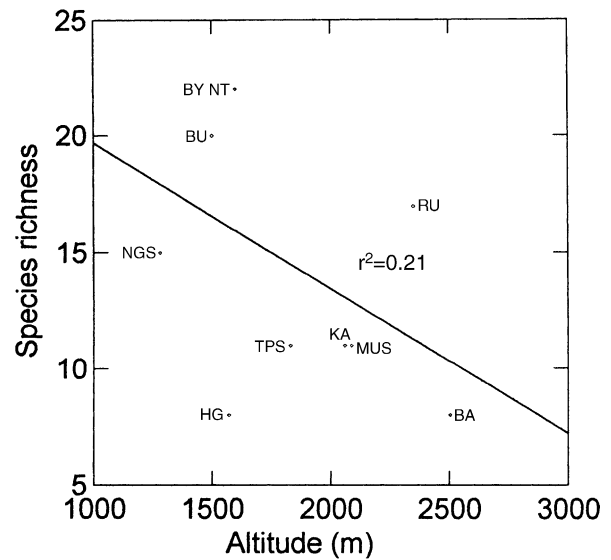


Fig 1 Scatter plot of species richness against altitude in metres. Species richness refers to the number of species recorded at each site. Altitude refers to the height above sea level. From a regression analysis, altitude explains 21 % of the variation in species richness.

always more than the shrew species. The number of individuals trapped at each site was found to correlate positively with trap effort ($r_s = 0.8, P < 0.02$). The slope of the regression line between altitude and trap success was negative, indicating a reduction in trap success with altitude. A regression analysis of species richness with altitude was negative (Fig. 1), indicating a reduction in species richness with altitude. From the value of r^2 (coefficient of variation) it was apparent that altitude accounts for 21 % of the variation in species richness with altitude.

The Shannon–Wiener index of diversity was highest at Byumba, at 2.348 and lowest at Hamuhingo grassland, 1.69 (Table 3). A regression analysis of species diversity

Table 2 Record of species richness, trap success, and altitude by site

Site	RU	BU	TPS	BY	NGS	NTF	HG	BA	MUS	KA
Altitude (m)	2350	1500	1830	1541	1280	1600	1571	2503	2088	2060
Trap nights	981	1937	626	1177	1106	2455	1200	1200	1210	1200
Trap success (%)	8.7	5.6	7.5	11.4	5.6	8.27	3.58	2.25	4.38	3.41
Species richness	17	20	11	22	15	22	8	8	11	11
Shrew species	3	4	3	4	5	6	2	2	3	3
Rodent species	14	16	8	18	10	16	6	6	8	8

Trap nights is the trapping effort employed at each site to survey the rodents and shrews fauna. Trap success refers to the number of animals trapped per 100 trap nights. It gives an indication of the productivity of the communities sampled in that the higher the trap success the higher the productivity of a given habitat.

Table 3 Shannon–Wiener diversity index (H'), evenness and number of species per 100 trap nights

Site	RU	BFR	BDG	TPS	BYF	BYD	NGS	NTF	HGR	BAM	MUS	KAS
H'	1.972	1.755	2.07	1.847	2.348	1.961	2.27	2.08	1.69	1.88	1.82	1.93
E_1	0.822	0.880	0.746	0.802	0.889	0.724	0.859	0.708	0.868	0.903	0.788	0.804
TRs	1.12	1.02	1.39	1.59	2.15	2.85	1.26	0.77	0.58	0.66	0.83	0.92

H' is the Shannon–Wiener index of diversity. H' increases with the number of species in a community.

E_1 is the evenness value and it indicates how the species are distributed in a community. Where the evenness is high, the mammal fauna is diverse and the species are equally abundant.

TRs refer to the number of species trapped per 100 trap nights.

with altitude was negative, indicating that the species diversity of small mammals decreases with an increase in altitude. Altitude accounted for 13% of the observed variation in species diversity with altitude. The number of species caught per 100 trap nights ranged from one to three species (Table 3), but the values do not give a clear indication of the productivity of the habitats.

Species cumulative curves for all sites sampled were drawn, and all showed an increase in species richness with increasing trap effort. For sites such as Ruhija forest, Byumba degraded habitat and Ngoto swamp, where a plateau was not attained, it is probable that further trapping could add to the species lists of those areas, and where the plateau was attained and maintained for at least 3 days such as in Buhoma degraded habitat, Buhoma forest, Kasiresire forest and at Hamuhingo grassland, the

sampling effort could be assumed exhaustive and representative of the small mammal communities of the sites.

Habitat preference

Lophuromys flavopunctatus was found to occupy all sites sampled, whereas certain species showed a preference for certain habitat types. *Colomys goslingi* and *Malacomys longipes* for example, were mainly trapped near water or in wet habitats. The Grey-bellied Pygmy mouse *Mus triton* and the Tropical groove-toothed rat *Otomys tropicalis* were only found in the grassland. Certain species of rodents and shrews were common at high altitudes, while others were common at low altitudes. *Lophuromys woosnami*, an Albertine rift endemic, was found to be most abundant at high altitudes above 2000 m. At lower altitudes it was replaced by *Lophuromys flavopunctatus* as the dominant species.

Discussion

The Bwindi Impenetrable National Park supports a very diverse community of rodents and shrews. Indeed, 67 species were confirmed to occur, of which 26 are new to the Park's record. The main factors accounting for the observed diversity could be the wide altitudinal range and the concomitant complex array of vegetation types.

In the grassland, we recorded a low number of species (eight) compared to other sites sampled and had the lowest species diversity ($H' = 1.69$). These findings indicate that the forest habitat supports more species than the grassland. These results concur with those of Hayward & Phillipson (1979), who found that grasslands usually contain fewer species of rodents and shrews than forests.

Species diversity was higher in the disturbed habitats and/or degraded forest than in the primary forest. Similar conclusions were arrived at in other studies: Delany

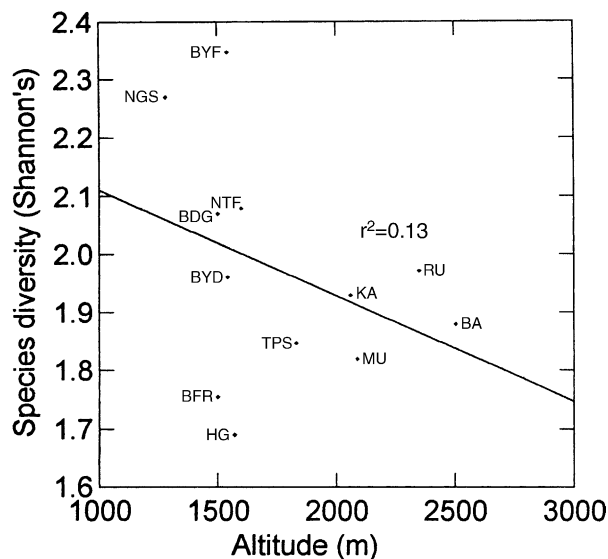


Fig 2 Graph of variation in species diversity with altitude, indicating that altitude accounts for 13% of the variation in species diversity.

(1971), Jeffrey (1977) and Muganga (1989). The ability of many species to coexist in degraded habitats can be attributed to the presence of several microhabitats and their diverse resources. Areas of forest relics interspersed with dense vegetation and several phases of regenerating forest might have provided numerous microhabitats for different small mammal species, leading to the observed diversity. Isabirye Basuta & Kasenene, (1987) suggested that the dense understorey of degraded forest at Kibale had more food resources for rodents and shrews at ground level and that it provided more protective cover and nest sites than the relatively sparse understorey of mature forest. Further evidence in support of the above assertion is derived from Delany (1971) who found that forest degradation at Mayanja forest resulted in a richer small mammal fauna, without necessarily eliminating any of the typical forest species. In this study, forest species such as *Praomys jacksoni* were found in degraded forest coexisting with nonforest species.

Bwindi National Park is unique in that it spans a wide altitudinal range from 1160 to 2607 m. As a result, it has a continuum of habitats from lowland to montane forests, each with a characteristic small mammal fauna. Understanding the biological mechanisms underlying different types of zonation allows a prediction of how these major patterns of biodiversity on landscapes will change through time (Huston, 1994). Austin & Smith (1989) contended that altitude *per se* has no direct influence on small mammal distribution; it is a 'factor complex' gradient. Altitude is correlated with a variety of resources and regulators that affect small mammal diversity, including precipitation and temperature.

The number of species was found to decrease with increasing altitude. The relationship between altitude and species richness has been examined in the rodents of Western Rwenzori (Misonne, 1963). Here, the number of rodent species declined from 35 at the base (700 m) to 3 at 4400 m and none at 4700 m. The small mammals of Bwindi fit the Rwenzori phenomenon accurately, in that diversity and richness were higher at lower altitudes compared to higher altitude habitats. According to Happold & Happold (1989), changes in altitude are associated with several important biological changes in Africa. The climate becomes progressively more temperate and alpine as altitude increases, with seasonal or regular frosts at night. These changes in altitude result in a series of vegetation zones. They further argue that increasing altitude results in a decline in grass biomass and growth,

a decrease in the number of small mammals, and the numerical dominance of a single species of small mammals also decreases with increases in altitude. This was found to be true for Bwindi, in that the numerical dominance of a species within a given community decreased with an increase in altitude. For instance at Buhoma (1500 m), the relative abundance of *Lophuromys flavopunctatus* was 42%, it fell to 13% of the community at Mubwindi swamp (2070 m), and 7% at the highest elevation (2503 m) sampled. The difference in relative abundance of this species at Buhoma and Bamboo zone was highly significant ($\chi^2_{(1)} = 25, P < 0.001$). However, the species *Lophuromys woosnami* showed an opposite trend to that of *L. flavopunctatus*, its relative abundance increasing with an increase in altitude. This difference may be attributed to the fact that at high altitude, *L. woosnami* becomes a better competitor and is adapted to living in the unique microhabitats available.

Endemism is critical to the understanding and conservation of biological diversity, since areas with high rates of endemism tend to have high species diversity. The small mammals of Bwindi show high rates of endemism compared to other forests in Uganda, excluding Rwenzori. The high rate of endemism could be attributed in part to its location near the Pleistocene Refugia. The basic idea of the refuge theory (Hamilton, 1982) is that certain restricted areas, generally mountain ranges with high precipitation, have continuously supported the same vegetation type (with associated fauna) throughout the periods of generally unfavourable climatic conditions that have been associated with glacial cycles over the past two million years.

The refuge theory is relevant both to an understanding of current distribution patterns and to the evolution of tropical species, because of isolation and subsequent allopatric speciation. Two of the 10 endemic species *Paracrocridura maxima* and *Sylvisorex vulcanorum* are of conservation concern (Nicoll & Rathbun, 1990). Little is known about the species *P. maxima*. Delany (1982) commenting on the number of exclusively forest species of rodents in various forests in East Africa, hypothesized that these faunas have probably originated from the eastern Congo forest with a progressive eastward decline in species numbers. This assertion holds true if Bwindi is compared to Kibale Forest. The latter forest is located further away from eastern Congo than Bwindi, and is currently known to have 25 species of small mammals compared to 67 species in Bwindi. Bwindi is rich in other

endemics: 10 species of plants (Howard, 1991), 8 butterfly species (Omoding, 1992) and 18 endemic species of birds (Keith, 1980). Therefore this makes Bwindi Afromontane forest island a unique biodiversity hotspot and among the highest conservation priorities in the Albertine Rift.

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