

Appendix 3: Table showing mean scores calculated from Timed Species Counts (TSCs) for amphibians in the various sites in the Rwenzori mountains/Semliki forest region sampled.

SPECIES/SITES	Ru	Se	Ny	'A'	'B'	Ma	Ka	Bu
01. <i>Africastus quadrivittatus</i>	1.43	1.39						
02. <i>Bufo kisoloensis</i>		0.28		0.25		0.29		
03. <i>Bufo maculatus</i>		0.39						
04. <i>Bufo regularis</i>	2.58	0.67	1.87					
05. <i>Hylarana albolabris</i>	5.22	2.72						
06. <i>Hyperolius cinnamomeiventris</i>	5.07		5.87	1.38				
07. <i>Hyperolius lateralis</i>			4.99	5.88				
08. <i>Hyperolius nasutus</i>			1.50					
09. <i>Hyperolius pussilus</i>			1.18	1.75				
10. <i>Hyperolius viridiflavus</i>			0.84					
11. <i>Kassina senegalensis</i>	1.72							
12. <i>Leptopelis christyi</i>		0.17						
13. <i>Phrynobatrachus acridoides</i>			3.00	0.38	5.50			
14. <i>Phrynobatrachus dendrobates</i>				0.50	3.33	0.71		
15. <i>Phrynobatrachus natalensis</i>	0.43	0.39	9.05	10.13	9.83	1.29		
16. <i>Phrynobatrachus plicatus</i>				0.13				
17. <i>Phrynobatrachus graueri</i>			0.33					
18. <i>Ptychadena mascareniensis</i>	1.79	1.67						
19. <i>Ptychadena porosissima</i>	0.29	4.00						
20. <i>Ptychadena chrysogaster</i>		0.34						
21. <i>Rana angolensis</i>		0.56	0.54	1.00	1.67	4.00	2.50	3.05
22. <i>Rana occipitalis</i>		1.17						
23. <i>Rana rwenzorica</i>								

Where: Ru = River Ruugo, Se = Sempaya hot-springs, Ny = Nyakarengija swamp, 'A' stream 'A', 'B' = stream 'B', Ka = River Kamatwe, Bu = Bujuku ridge.

SMALL MAMMALS ALONG AN ELEVATIONAL GRADIENT IN RWENZORI MOUNTAINS NATIONAL PARK, UGANDA

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SUMMARY

During 1990 and 1991, zoologists from Makerere University (Kampala) and the Field Museum of Natural History (Chicago) conducted surveys of the small mammal community in Rwenzori Mountains National Park. Surveys were conducted along an elevational transect, along the Mubuku and Bujuku Rivers. Over the course of 2 field seasons, surveys were conducted at 5 main camps and two smaller ones. Results are compared to the British Museum Expedition of 1905-06, the only other published comprehensive survey of small mammals on the eastern slope. Data are presented relating to habitat associations, relative abundance, activity patterns and elevational range. For select taxa, additional data are presented relating to size variation, reproductive condition, and demographics. Six species of small mammals are added to the Rwenzori list. Although our survey was comprehensive on a local scale, many species either known or described from the Rwenzori, were not documented. Biogeographic and conservation implications are discussed.

METHODS

Surveys in the first season (November-December, 1990) were conducted at three camps: Kyoha River (1960 m), Mahoma River (2075 m) and Nyabiataba (2700 m). W. T. Stanley coordinated the 1990 small mammal field efforts, working with R. M. Kinyo and R. L. Lubajo. During the second season (April-May, 1991) surveys were conducted at four main sites: Kyoha River (1960 m), Nyabiataba (2700 m), John Male (2400 m) and Lake Bujuku (2000 m); smaller collections were made at Mahoma River (2075 m) and Lake Mahoma (3000 m). Kerbis Peterhans coordinated the 1991 small mammal field activities, working with P. K. Austin, Kinyo, and Lubajo.

The retention of voucher specimens is fundamental to such surveys (see Appendix for discussion). Most small mammals were collected with Sherman live traps. Museum Special snap traps and Victor Rat traps. A single trap placed out for one night was equal to one trapnight. A variety of baits were employed including fish, worms, and peanut butter and oats.

Bats were collected from mist nets. Mist net effort is reflected in the Rwenzori bird paper (Willard et al., this volume). Most of the smaller shrews (<10 grams) were caught with pitfall traps. In this method, 5 liter buckets are buried into the soil so that their rims are flush with the ground; window screen netting connected the buckets across the midline (e.g. Voss & Emmons 1996, Fig. 7; Stanley et al., 1996). Buckets are placed 4-5 meters apart. Pitfall nights are recorded by dividing the length of the 'netting' by 10 meters. A thirty meter length of screening would translate to 3 pitfall nights.

Giant rats (*Cricetomys emini*) were collected with Conibears, local snarls, Tomahawk live traps, and Victor Rat traps. Small carnivores ($n=5$) and hyrax ($n=5$) were collected with Conibears. Two squirrels (*Funisciurus c. carruthersi*) were collected from local Baluku Kanerya originating from the settlement of Ruboni, located on the left bank of the Mubuku River at an elevation of 5700ft.

Data on trap nights, habitat, and activity patterns are available for the 1991 field season. Animals retrieved from the traps in the morning were considered to have been nocturnal. Those recovered during the late afternoon were considered to have been diurnal. The proportion of diurnal captures is typically underestimated as it could take one hour to reach certain traplines; some nocturnal activity could be documented as diurnal activity.

Several fortuitously gathered and/or commensal specimens are not included in some totals: these include one *Hylomyscus d. denitiae* and four *Lophuromys flavopunctatus* collected at Bigo Bog and 13 *Hylomyscus d. denitiae* and 7 *Lophuromys flavopunctatus* collected within Bujuku Hut.

For the British Museum expedition, elevational data on small mammal occurrence were published in Woosnam (1909-1910) and Thomas & Wroughton (1910). There are conflicts between Woosnam's report and the data provided by Thomas and Wroughton (1910). Several species are not included in the Grass Zone in our tables as they are recorded by Thomas & Wroughton (1910) at 6000ft and above. However, Woosnam states (1909-1910) that the Forest Zone begins at 6500ft which implies that taxa found at 6000ft may occur in the Grass Zone. We include only those species listed by Thomas and Wroughton from 5,000ft and below, to be from the Grass Zone. Since this situation is problematic, the distinction between the Grass Zone and Lower Forest Zone small mammal faunas is not clear.

Dendromus insignis, is listed by Woosnam (1909-10) as occurring in the Forest-Zone (6500-8500ft) whereas the only specimen recorded by Thomas and Wroughton is listed as from 10,000ft. Here, we place this specimen in the Bamboo Zone at 10,000ft. *Chrysocloris stuhlmanni* is listed by Woosnam as representative of the Tree-Heath and Moss-Zone (10,000-12,500ft) whereas Thomas and Wroughton, quoting Woosnam himself say only it is found as high as 10,000ft (p. 493). *Myosorex blarina* is also included by Woosnam in the Bamboo and the Tree-Heath and Moss-Zone whereas Thomas and Wroughton, state that it was only recovered at 10,000ft. Indeed both specimens were recovered at the same place (Thomas and Wroughton, p.490). This elevation is within the bamboo zone, falling well below the Tree-Heath and Moss-Zone. Despite these inconsistencies, the only specimen which effects the elevational range of the Rwenzori species is the single record of *Dendromus insignis*.

Mammalian nomenclature follows Wilson and Reeder (1992) with the following exceptions. We follow Van der Straeten and Dudu (1990) who demonstrate the unique status of *Praomys jacksoni montis* (Thomas and Wroughton, 1910). However, future multivariate analyses may demonstrate the occurrence of two species of *Praomys* in our collection. We consider *Hybomys lunaris* to be restricted to the Rwenzori as this taxon was resurrected on the basis of material collected in more southerly Mountains of the Albertine Rift (Van der Straeten, personal communication; Van der Straeten, et al., 1986). Based on published accounts, the following taxa are

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recognized: *Roussettius angolensis ruwenzorii* (Eisenbraun, 1965), *Rhinolophus macclaudi ruwenzorii* (Smith and Hood, 1980), *Hylomyscus denitiae vulcanorum* (Bishop, 1979). Based on unpublished surveys of adjacent mountain tops and historical museum records, we recognize the following sub-species *Sylviores granii granii*, *Sylviores lunaris lunaris*, *Otomys denti denti*, and *Otomys typus darmouthi*. If we do not recognize subspecies we use the code 'ssp'.

Age was estimated using both body weight and dental wear. Using plots of body weight versus cranial metrics, juvenile status was estimated using the following weights: *Mus bulyi* < 8 grams, *Hylomyscus denitiae* < 20 grams, *Lophuromys woosnami* < 30 grams, *Lophuromys flavopunctatus* < 35 grams, *Praomys jacksoni montis* < 35 grams. For all taxa, individuals were considered to be juvenile if they displayed dental wear stage 3 or less (sensu Verheyen and Bracke, 1966).

We use the following abbreviations for our campsites: Ky (Kyoha River), Ma (Mahoma River), Ny (Nyabihaba), LM (Lake Mahoma), JM (John Mate), Bu (Lake Bujuku).

Habitats Sampled

In his review of the British Museum expedition of 1905-1906, Woosnam (1908) discussed numerous vegetation zones on the Ugandan slope of the Rwenzori. Woosnam describes the foothills of the Rwenzori as belonging to the Grass-Zone (3000-6500ft), starting with short grass plains with scattered acacia and euphorbia, merging into elephant grass (*Pennisetum purpureum*) and *Hyparrhenia* spp. in the upper reaches (5,000-6500ft). On the slopes, thorny *Erythrina abyssinica* is conspicuous (Osmaston & Pasteur, 1972). Today, this zone is heavily cultivated. The common crops include cassava, millet, cooking bananas, beans, sweet potatoes and taro (Ibid.). Our group did not sample this habitat.

The British Museum expedition also sampled the animal communities in the dry plains just beyond the foothills of the mountain range. These specimens originate in the acacia woodland and open habitats of Muhokya ('Mokya' of Woosnam, 1909-1910, fig. 1) at an elevation of 1000 meters (3280ft). Coincidentally, Delany (1964) collected 413 small mammals in the adjacent area of Queen Elizabeth National Park. The habitats he sampled are mostly grass savannah (*Imperata cylindrica* and *Cymbopogon afrondatus*) sometimes associated with semi-deciduous thicket. Smaller collections came from semi-deciduous forest (Maramaganbo with *Cynometra* sp. and *Celtis* sp.) and herb swamp. We did not sample this habitat.

Within the Rwenzori proper, both the British Museum Expedition and our surveys started along the Mubuku River. At the confluence of the Bujuku River however, our expedition followed the established hiker's routes and continued up the Bujuku whereas the British Museum expedition sent forays up the Mubuku River (Wollaston, 1908). According to Woosnam (1909-1910), the Forest-Zone begins at 6500ft, the lower margins of which include substantial trees (*Symphonia globulifera* and *Elaeodaphnogramma utile*). Tree ferns (*Cyathea decurva*) are common and *Impatiens* spp. are plentiful near streams. The base camp for the BMNH expedition was in this area and was occupied for four months. Wollaston (1908) refers to this base camp as 'Bihunga' at an elevation of 6500ft (=1980m), formerly the site of a small

'village' of three native huts. Uganda survey maps (Sheet 66/1, 1:50,000, Lands and Surveys Department, 1958) represent this site as 'Mihunga', a small plateau at 6800ft, located just below the confluence of the Kyoha (= Choha) River. Later, Loveridge was to establish his camp at this very place (Allen & Loveridge, 1942).

We established camps in the lower section of the forest zone at the confluence of the Kyoha River (1920m) and at the confluence of the Mahoma River (2100m). Both camps were located on the right bank of the Mubuku River, just upstream from the actual confluence. The Kyoha site was surveyed on two occasions, 10-18 November 1990 and 8-14 April 1991. The Mahoma River site was predominantly surveyed 19-30th November, 1991; a smaller collection ($n=24$) was made 3-9 May, 1991.

According to Woosnam, the upper reaches of the "Forest-Zone" are marked by the occurrence of a single conifer, *Podocarpus milanjianus*, which appears around 7500ft but becomes most plentiful as the bamboo zone (8500ft) is reached. In the open valleys, bracken ferns (*Pteridium aquilinum*) and thorny blackberries (*Rubus transvaalicus*) can dominate as they do just above Nyabibaba. Our camp at this point was located at the rest area, known as Nyabibaba (2670m = 8750ft) a ridge formed by a glacial moraine just below the confluence of the Mubuku and Bujuku Rivers on the right bank of the Mubuku. Wollaston (1908) refers to this site, the site of an "immense erratic boulder", still in place, as 'Viaba' or 'Naktiawa'. Our group surveyed this site on two occasions; 2-12 December 1990 and 15-22 April 1991. We consider the area of Nyabibaba to be the upper reaches of the "Forest-Zone" as the once heavy bamboo stands have been transformed into a dense tangle of climbers and degraded bamboo.

The Bamboo-Zone, beginning at 8500ft (per Woosnam) is currently heavily degraded but was apparently more substantial at the time of the BMNH expedition. The BMNH considered the area around Nyabibaba as part of the bamboo zone (*Arundinaria alpina*) which Woosnam defined as 8500-10,000ft (2590-3050m). Wollaston (1908, p.85) describes the area: "After leaving the big rock, Viaba, the track plunged almost at once into the bamboos" (p.85). Today, the degraded bamboo is intermingled with thick tangles of *Mimulopsis elliptica* as one leaves Nyabibaba for Lake Mahoma. At Nyabibaba, the first tree heath occurs in the form of *E. (P.) johnstonii* (Osmaston & Pasteur, 1972) as does the first Lobelia. In 1991, we found the purest stands of bamboo in the vicinity of Lake Mahoma (2960m = 9700ft), which we accessed from our camp at Nyabibaba. *Erica (Philippia) kingaensis* also makes its first appearance in the bog adjacent to Lake Mahoma (Osmaston, personal communication). We include only those specimens caught in the vicinity of the pure Lake Mahoma bamboo stand (3000m) to be originating from the "Bamboo-Zone".

Above Nyabibaba, we followed the course of the Bujuku River. The British Museum expedition sent forays up the Mubuku River (Wollaston, 1908). The British Museum Expedition undertook shorter 8-10 day excursions up the Mubuku from their base at 'Bihunga' (Woosnam, 1907). Our sample of the ericaceous zone was centered on the newly constructed tourist hut known as John Mate Camp (3370m), located on the left bank of the Bujuku River, midway between the former shelters known as Bigo and Nyamuleju. Woosnam terms this zone the "Tree-Heath-and-Moss-Zone" (10,000-12,500ft = 3050-3810m). This site was surveyed by us on one occasion, for 9 days, between 24th April and 2nd May 1991.

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Our sample of the Senecio-and-Lobelia-Zone was centered on the hut known as Bujuku, above Lake Bujuku at an elevation of 3980m. Woosnam's range for this zone extends from 12,500-14,500ft (3810m-4420m). We camped at Bujuku on one occasion between 2nd May and 8th May, 1991. Neither we nor the BMNH surveyed the Snow-Zone (14,500-16,800ft). We did however proceed through the Stuhlmann Pass where we recovered specimens from a poacher's camp at 13,600ft.

RESULTS

Activity Patterns

Although most species are nocturnal, there are important exceptions (Table III). Eighty-eight per cent of the *Hybomys lunaris* ($n=17$), 65% of the *Lophuromys flavopunctatus* ($n=84$), and 38% of the *Mus bufu* ($n=42$) were captured during the day. Many of the large grass/sedge-dwelling rodents were caught during the day: *Dasyms montanus* (5/8), *Oromys typus darwini* (6/15) and *Oromys denti denti* (1/4). Surprisingly, four of the shrew species, *Sylvisorex grani* (4/12), *Myosorex blarina* (1/3), *Crocidura montis* (2/3), and *Crocidura oliveri* (1/5) exhibited diurnal activity. Stanley et al. (1996) caught 50% ($n=4$) of their *Crocidura oliveri* sample during the day.

Reproductive Seasons and Demographics

Data on pregnancy for each species are presented in Table IV and age profiles for select taxa in Table V. Several species show a higher rate of pregnancy during the rainy season (Nov/Dec, 1990 vs. April/May, 1991). These include *Hybomys d. deniae* (28% vs. 16%) and *Lophuromys flavopunctatus* (25% vs. 11%). Other species show the reverse pattern including *Praomys jacksoni montis* (20% vs. 35%), *Lophuromys woosnami* (14% vs. 44%) and *Mus b. bufu* (12% vs. 43%). Nearly 50% of the *Roussettus angolensis ruwenzorii* were pregnant in Nov/Dec 1990. *Cricetomys emini* was not pregnant ($n=10$) either season. There may be seasonal differences in the timing of reproduction in the congeners *Oromys d. denti* and *Oromys typus darwini*, with the later reproductively active in April/May. For other species, data are inadequate to document seasonal differences.

Twice as many *Hybomys d. deniae* juveniles were documented in 1991 while *Lophuromys woosnami* had proportionately more juveniles in 1990. The relatively few captures of *Lophuromys woosnami* in 1991 suggests a die-off in the interim.

We assumed that the relatively high number of pregnancies and fewer juveniles observed in Nov/Dec 1990 would result in observing fewer pregnancies and a higher number of individuals, particularly juveniles, in April/May, 1991. This prediction is based on assumptions of gestation and weaning which would need verification through longevity studies in captivity. The assumption apparently holds true only for *Hybomys d. deniae*. In 1990, based on dental criteria, 20% were classified as juveniles; this figure doubled to 40% in 1991. If body weight data are used to define age, similar increases are obtained. Nearly twice as many females were with embryos in 1990 (Table IV) suggesting that the high pregnancy rate of Nov/Dec provided the high juvenile cohort documented in 1991.

The inverse pattern holds for *Lophuromys woosnami* (Tables IV and V). Relatively few pregnancies were recorded in Nov/Dec (14%). This resulted in an older age cohort (100% adults) with fewer individuals during the April/May census (Table VI). Between December 1990 and April 1991, the demographic profile increased in age as relatively few births occurred. A decrease in the absolute population of *Lophuromys woosnami* during this interval suggests attritional mortality. The pregnancy rate rose to 44% in April/May.

The demographic data for several species are hard to interpret. The smallest murine, *Mus bryo* may have such rapid turnover that the coarse seasonal differences we are able to document (a 5 month gap between surveys) are inadequate to distinguish demographic changes. The data for *Praomys jacksoni montis* and *Lophuromys flavopunctatus* do not appear to be significantly different from season to season. It is possible that two taxa of the *Praomys jacksoni* group (*sensu* Van der Straeten and Dudu, 1990) are present in the Rwenzori thereby confounding our ability to document ecological, demographic and behavioral affinities. As an additional variable, most *Lophuromys flavopunctatus* were captured at higher elevations in 1991. Data for *Lophuromys flavopunctatus* and *Mus bryo* yield different demographic results depending on ageing methodology, also suggesting statistical insignificance.

New Rwenzori Records

As a result of these surveys, six species are added to the Ugandan Rwenzori small mammal list (*Pipistrellus kuhli fasciatus*, *Miniopterus inflatus*, *Myotis welwitschii*, *Sylvisorex vulcanorum*, *Crocidura dolichura*, and *Dendromus kivu lunaris*). Two of the bat species from these surveys are new records for the country (Stanley, et al. 1996). Although this survey appears comprehensive, many small mammal species, either known or described from the Rwenzori, were not documented in our 1989-90 surveys (*Chrysorchloris stuhlmanni stuhlmanni*, *Microptamogale ruwenzorii*, *Paracrocidura maxima*, *Ruwenzorisorex suncoides*, *Dasyms incomtus medius*, *Grammomys dryas*, *Tranomys venustus*, *Neus ruon joris*).

Elevational Distribution

Raw data on small mammal elevational distribution for the 1990 and 1991 field seasons are presented in Table VI. Data for both field seasons is combined in Table VII. Finally, our data is merged with that from the British Museum and is presented in the form of presence/absence data (Table VIII).

Small mammal communities in the Rwenzori are clearly defined. Below the forest line, in the Zone of 'Elephant Grass', the British Museum expedition documented many species assumed to be typical of this habitat: *Epomophorus labialis auratus*, *Myotis hispida*, *Pipistrellus nanus*, *Africanus niloticus ssp.*, *Grammomys dryas*, *Lemniscomys striatus ssp.*, *Mastomys hildebrandtii ssp.*, *Mus musculoides graia*. We collected none of these species as we did not sample the 'Elephant Grass'. Three of these species were also encountered by the British Museum expedition in the lowermost reaches of the forest zone but this may be due to the location of a native settlement at their forest camp site of Bihunga at that time. Additionally, several species were collected at 'Mokia' (Mohokya), a site on the acacia savannahs of the adjacent Queen

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Elizabeth National Park. These species include *Lavia fons*, *Taera valida*, *Lemniscomys maculatus*, *Rattus rattus*, and *Graphiurus microtis*.

In the lowermost forested habitats, *Praomys jacksoni montis* is the most dominant species, comprising 50% and 45% of the rodents at our two camps (Kyoha R., Mahoma R.). *Graphiurus murinus ssp.* is also restricted to this zone but the sample size is small ($n=3$, FMNH; $n=3$, BMNH). Both species disappear completely in the higher reaches of the forest zone. Other common rodents in the lower forest zone include *Mus bryo* ($n=74$, 16%), *Hybomys lunaris* ($n=47$, 10%), and *Lophuromys woosnami* ($n=40$, 9%). Shrews, represented by three genera and seven species, have their highest diversity in the lower forest zone. Two species (*Crocidura dolichura* and *C. nibe*) were only collected at this elevation.

A major rodent turnover occurs at the level of Nyabihaba, which we consider to be the upper reaches of the forest zone. The once dominant *Praomys jacksoni montis* has completely disappeared. Squirrels, the giant rat *Cricetomys*, four additional murines (*Hybomys lunaris*, *Lophuromys woosnami*, *Mus bryo*, and *Oenomys hypoxanthus*), and two shrews (*Crocidura olivieri ssp.*, *Sylvisorex vulcanorum*) make their final appearance at Nyabihaba. The 'shrew-mouse' *Lophuromys flavopunctatus* also emerges as a dominant species, now representing 35% of the rodent fauna (vs. 3% in the lower forest zone). Insectivorous bats were not observed frequently within the forest zone. Of the four species encountered, none were found above Nyabihaba. Both species of *Rousettus* were present, although Nyabihaba was the highest elevation we encountered *Rousettus angolensis*.

Our sample of the Bamboo Zone was inadequate. Our limited data ($n=14$) suggest the rodent community is quite similar to the upper forest zone near Nyabihaba with *Lophuromys flavopunctatus* and *Hybomyscus denitiae* well represented. However, *Lophuromys w. woosnami* is especially common in the solid bamboo stands. A special effort was made to capture shrews with pitfalls in the mesic habitats around Lake Mahoma. Our first record of the montane endemic *Crocidura montis* is from here but the BMNH expedition did record this species in the lower parts of the forest zone.

The small mammal fauna of the Tree-Heath and Moss Zone at 3400m (John Mate Camp) appears to be identical to the impoverished fauna from the Senecio and Lobelia Zone at Lake Bujuku. *Hybomyscus denitiae* and *Lophuromys flavopunctatus* continue to dominate in number (39% and 25%). New additions include *Dendromus nigritis*, the first multi-individual record of *Dendromus kivu* and the debut of the Rwenzori endemic, *Otomys typus darlmouthi*. *Rousettus lanosus* occurs in high numbers, as many occupy the nearby cliffs. After incorporating the British Museum records, the small mammal fauna is identical in the Senecio-Lobelia Zone of Lake Bujuku (one possible exception being *Chrysorchloris stuhlmanni*).

DISCUSSION

Species Replacement

In order to interpret the abundant rodent data, we have lumped the rodent and bat species into groups (Table IX) which reflect our preliminary interpretations of their co-variation. These groups are determined by combinations of guild, niche and systematic relationship.

The displacement of *Roussettus angolensis rwenzori* by *Roussettus lanosus* *lanosus* may be due to roosting preference. *Roussettus lanosus* only roosts in caves, such as are found in the open cliffs above tree line, while *R. angolensis* prefers to roost in trees (Kingdon, 1974). *R. angolensis* may therefore be limited by the tree line which is why it may not occur above Nyabihaba. As there is no fruit in the upper elevations where it roosts, *R. lanosus* makes daily excursions to lower elevations to forage (Thomas and Wroughton, 1910).

It is possible that *Hybomys lunaris* (dropping from 12% to 2%) is replaced at Nyabihaba by the diurnal *Lophuromys flavopunctatus* (rising from 3% to 35%) but it is not clear if this may be due to a common body size and activity pattern (both diurnal, 40-50 grams) or to similar diets, as both can be insectivorous (Delany, 1975). Stomach contents are available to resolve the issue. The insectivorous *Lophuromys flavopunctatus* (Hart 1940, Delany 1964) might be expected to fill the void vacated by a less diverse shrew community at Nyabihaba (which has dropped to 4 taxa) but the largest shrews are still plentiful (e.g. the 25-30 gram *Crocidura olivieri*).

Praomys jacksoni montis is apparently supplanted by the related taxon, *Hybomys d. denitiae* which rises to 38% of the fauna (from 5% in the lower forest zone). These numerically dominant, nocturnal murines, were once considered to be congenetic (Misonne, 1974); they are currently considered to be closely related (Chevret et al. 1994).

By definition, above tree line (Nyabihaba), numerous forest species disappear. There appears to be little difference between the faunas of John Mate and Bujuku, so data are combined. Two new guilds of stenocephalic (narrow-headed) rodents appear, replacing the forest taxa in the now open moorland. One guild includes the species *Dasyms montanus*, *Otomys typus darmowhi*, and *Otomys denti denti*. All three species are herbivorous, vole-like, large-bodied, thickly furred, short-tailed, and long-clawed. They represent 20% of the rodent fauna (Table IX) at this elevation. None of these species represented more than 1% of the rodent fauna at lower elevations.

The second stenocephalic guild is represented by the *Dendromurinae* *Dendromus kivu* and *Dendromus insignis*. These species with their small, light build, prehensile tails and specialized cheiridia are thought to be grass-seed specialists clambering about on thin vertical supports (Kingdon, 1974). These two species represent 16% of the small mammal fauna at John Mate, 10% at Bujuku Hut. Only one *Dendromurine* was captured at lower elevations.

Similar patterns have been shown in the moorland of Ethiopia where the endemics *Otomys t. typus*, *Stenocephalymys albocaudata*, and *Dendromus loyai* are restricted to the ericaceous and moorland zone (Yalden, 1988). In describing the genus *Stenocephalymys*, Frick states, "The form most nearly approaching the new genus in its peculiar orbital constriction is *Dasyms*" (1914, p. 7). In the moorlands of Ethiopia, *Stenocephalymys* may be the ecological vicar of *Dasyms*.

The stenocephalic condition facilitates dorsal rotation of the orbits, which, in an open country, is conceivably useful in avoiding aerial predators (e.g. owls). It is relevant to note that all three Rwenzori species are often diurnal (12 of the 18 individuals collected in 1991 were collected during the day; Table III). In the Bag Mountains, Yalden (1973) documented small mammal prey remains from

Abyssinian long-eared owl (*Asio abyssinicus*) beneath a giant heath at 3940m. Of the 92 individuals recovered, 73 (79%) were either *Otomys t. typus* or *Stenocephalymys albocaudata*. Clearly these plump rodents are subject to severe predation pressure; perhaps diurnal activity, as exhibited by our Rwenzori taxa, reduces this pressure. On the other hand, the Rwenzori *dendromurines* discussed here were all trapped at night.

Diversity, Endemism, Biogeography and Conservation

A common pattern in tropical montane systems is that of decreasing vertebrate diversity with elevation. This trend has been documented for birds in the Rwenzori (Willard et al., this volume; with references). For small mammals and other vertebrates, this pattern is common (Peterson et al. 1993; Peterson et al. 1989; Patterson et al., in press, with references). Unfortunately, our lowest camp already begins at a high elevation (1900m). Among our well-surveyed Rwenzori camps (Low Forest, High Forest, Heath, Senecio), small mammal species diversity decreases with elevation (from 33 species to 21 to 13 to 12). However, the proportion of endemic species increases (from 52% to 62% to 77% and 75%). These data suggest that conservation efforts need to target both mid-elevation forests and high elevation moorlands, in order to maximize the maintenance of biodiversity. Only the maintenance of continuous longitudinal transects will provide effective conservation solutions.

The Rwenzori are an area of immense importance in discussions of central African biogeography and small mammal alpha-taxonomy. Since 1894, a minimum of 38 taxa (33 small mammals) have been described from the Rwenzori and its foothills (summarized in Table X). Twenty-six of the 33 taxa remain valid, while 21, an extraordinarily high number, are Albertine Rift endemics (Table VIII). The relatively low overall number of taxa may be due to the likely long-term isolation of the Rwenzori as well as the absence of low to mid-elevation forests in the Mubuku River valley. Additional surveys, targeting lower elevation forests and grasslands, such as those on the NW slope, might provide additional species records.

Eight hundred and forty one of the specimens described here are topotypical. As such, they are essential for defining levels of variation within these taxa. Rwenzori collections serve as a baseline for comparison with other reputed taxa. Based on our surveys, and those from mountains to the south, a minimum of 6 taxa are now known to be restricted to the Rwenzori: *Myosorex blarina*, *Hybomys lunaris*, *Dasyms montanus*, *Hybomys denitiae denitiae*, *Praomys jacksoni montis*, and *Cephalophus rubidus*. This unique suite of mammals enables us to delineate a 'Rwenzori' subdivision within the Albertine Rift zone of endemism. Recognition of taxa and their geographic and elevational distribution, is the most fundamental component in biodiversity surveys and assessments. Sound conservation management decisions must be based on the distribution of these taxa.

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REFERENCES

- Allen, G.M. & A. Loveridge, A. 1942 Scientific results of a fourth expedition to forested areas in east and central Africa. I Mammals Bull. Mus. Comp. Zool. Vol 139 (4)
- Alper, D. 1995 Population ecology of small mammals of the Bwindi-Impenetrable National Park (BINP). M.Sc. Thesis, Zoology Department, Makerere University, Kampala, Uganda.
- Bishop, L.R. 1979 Notes on Praomys (*Hylomyscus*) in eastern Africa. Mammalia 43, 521-530.
- Camerano, L. 1906 *Felis pardus ruwenzorii*, subsp. n. Boll. Mus. Zool. ed Anat. Comp. Univ. Torino 21:545. 1-6.
- Chevret, P., C. Denys, J.-J. Jaeger, J. Michaux & F.M. Catzeflis 1993. Molecular evidence that the spiny mouse (*Acomys*) is more closely related to gerbils (*Certhiinae*) than to true mice Proc. Natl. Acad. Sci. USA 90, 3433-3436.
- Chevret, P., L. Granjon, J.M. Duplantier, C. Denys, & F. Catzeflis, 1994. Molecular Phylogeny of the Praomys complex (Rodentia: Murinae): a study based on RNADNA hybridization experiments. Zool. J. Linn. Soc., 112:425-442, 4 figs.
- Delany, M. 1964 An ecological study of the small mammals in the Queen Elizabeth National Park, Uganda Rev. Zool. Bot. Afr. LXX, 1-2, 129-147.
- Denys, C. & J. Michaux La troisième molaire supérieure chez les Muridae d'Afrique tropicale et le cas des genres *Acomys*, *Uromys* et *Lophuromys*. Bonn. Zool. Beitr. 43 (3), 367-382.
- Eisenrath, M. 1965 Der Rassenkreis *Roussetus angolensis* (Bocage) Bonn. Zool. Beitr., 16 (1/3), 3.
- Frick, C. 1914 A new genus and some new species and subspecies of Abyssinian rodents, Ann. Carnegie Mus., 9:7-28, pls. 1-5.
- Hall, R.T. 1940 Lagonomorphs and Rodentia other than Sciuridae, Anomaluridae and Idiuridae, collected by the American Museum Congo Expedition. Bull. Amer. Mus. Nat. Hist. 76.
- Hill, 1942 A new bat of the *Rhinolophus philippinensis* group from Mount Rwenzori, Africa. Ann. Mus. Novit., 1180:1-2.
- Honacki, J.H., K.E. Kinnman, J.H. Koeppl (eds.) 1982 Mammal Species of the World: A taxonomic and geographic reference. Lawrence: Allen Press.
- Kingdon, J. 1974 East African Mammals Vol IIB. Hares and Rodents. An atlas of evolution in Africa. Chicago: University of Chicago Press.
- Lomberg, E. & N. Gyldenstolpe, 1925. Preliminary diagnoses of seven new mammals. Ark. Zool. 17B, 5.
- Matschie, P. 1894 Drei neue Säugethiere (*Hesperes*, *Pedioragus*, *Chrysoschionis*) von Ostafrika vor. Sitzungber. Ges. Naturforsch. Freunde, Berlin, 121-125.
- Meester, J. 1990 The importance of retaining voucher specimens. In: Herholdt, E.M., ed., Natural history collections: their management and value, 123-127. Transvaal Museum Special Publication No 1, Pretoria: Transvaal Museum.
- Musser, G.G. & M.D. Carleton, 1993. Family Muridae, in: Mammal Species of the World, A Taxonomic and Geographic Reference. 2nd Ed. Washington: Smithsonian Institution Press.
- Neumann O. 1902 Proc. Zool. Soc. Lond. 2, 142-144.
- Osmaston, H.A. & D. Pasteur 1972 Guide to the Rwenzori. Mountain Club of Uganda.
- Osgood, W.H. 1936 New and imperfectly known small mammals from Africa. Field Mus. Nat. Hist. (Zool. Ser.) 20 (21), 217-256.
- Pocock, R.I. 1907 A monographic revision of the Monkeys of the genus *Cercopithecus* 677-746. Proc. Zool. Soc. Lond.
- Pocock, T.N. 1976 Pliocene mammalian microfauna from Langebaanweg: a new fossil genus linking the Oromyinae with the Muridae. S. Afr. J. Sci. 72, 58-60.
- Schwann, H. 1904 On new forms of *Anomalurus* and *Sciurus* from Tropical Africa. Ann. Mag. Nat. Hist. 7(13), 70-73.
- Stanley, W.T., S.M. Goodman & R. Hutterer 1996 Notes on the insectivores and elephant shrews of the Chome Forest: South Pare Mountains, Tanzania (Mammalia: Insectivora et Macroscelidae). Zool. Abh. Mus. Tierkd. Dresden 49, (8), 131-147.
- Stanley, W.T., J.C. Kerbis Peterhaus, R.M. Kityo, L. Davenport 1996 New Records of Bats for Uganda and Burundi. Afr. J. Ecol. 34, 196-201.
- Thomas, O. 1901 On the more notable Mammals obtained by Sir Harry Johnston in the Uganda Protectorate. Proc. Zool. Soc. Lond. 2, 85-90.
- Thomas, O. 1906 Descriptions of new Mammals from Mount Rwenzori 7(18), 136-147.
- Thomas, O. 1907 On further new Mammals obtained by Rwenzori Expedition 7(19), 118-123.
- Thomas, O. & R.C. Wroughton 1910. Rwenzori Expedition Reports. 17. Mammalia. Trans. Zool. Soc. Lond. 19, 481-518.
- van der Straeten, E. & A. Dudu 1990. Systematics and distribution of Praomys from the Masoko Forest Reserve (Zaire) with the description of a new species. Pp. 73-83. In Vertebrates in the Tropics (G. Peters and R. Hutterer, eds.) Bonn: Museum Alexander Koenig.
- Van der Straeten, W.N. Verheyen, & B. Harrie. The taxonomic status of *Hylomys univittatus* *luratus* Thomas, 1906 (Mammalia: Muridae). Cimbebasia, ser. A, 8, 209-218.
- Verheyen, W. & E. Bracke 1966 The influence of aging on the cranio-metrical characters of *Praomys jacksoni* (de Winton, 1897). Proc. of the Colloq. on African rodents. Ann. Mus. Roy. Afr. Centr., in-8°, Zool., 144.
- Voss, R.S. & L.H. Emmons 1996 Mammalian Diversity in Neotropical Lowland Forests: A Preliminary Assessment. Bull. Amer. Mus. Nat. Hist. 230.
- Watts, C.H.S. and P.R. Baverstock, 1995. Evolution in the Murinae (Rodentia) assessed by microcomplement fixation of albumin, Aust. J. Zool., 43, 107-116.
- Willard, D.E., T.P. Gnoske & R.M. Kityo 1998 An elevational study of the birds of the Mubuku and Bujuju River Valleys. Rwenzori Mountains National Park, Uganda. This vol.
- Wilson, D. & D. Reeder, 1992. 2nd ed. Mammal Species of the World: A Taxonomic and Geographic Reference. Wash DC: Smithsonian Inst. Press
- de Witte G.-F., & S. Frechkop 1955 Sur une espèce encore inconnue de mammifère Africain, *Potomogale ruwenzorii*, sp. n. Bull. Inst. R. Sci. Nat. Belg., 31(84), 1-11.
- Wollaston, A.F.R. 1908 From Ruwenzori to the Congo. London: John Murray
- Woodsam, R.B. 1909-1910 Ruwenzori Expedition Reports. 2. Itinerary. Trans. Zool. Soc. Lond. 19, 5-23.
- Yalden, D.W. 1988 Small Mammals of the Bale Mountains, Ethiopia. Afr. J. Ecol. 26, 281-294.
- Yates, T.L., W.R. Barber, D.M. Armstrong 1987. Survey of North American collections of Recent mammals. J. Mammal., Suppl. to 68(2):1-76.
- After the preparation of this paper the results of further collections of small mammals were published in: Howard, P.C., T. Davenport & M. Baltzer 1996 Rwenzori Mountains National Park: biodiversity report. Forest Department, Kampala.

TABLE I: Trap Success for 1991 Survey

	Trapnights	Animals	Trap Success
Kyoha River	1217	117	9.6 %
Maahoma River	180	14	7.8%
Nyabitala Camp	1197	125	10.4%
John Mate Camp	1245	68	5.5 %
Bigo Camp (1 night)	20	5	25.0%
Lake Bujuku	742	62	8.4 %
Lake Bujuku (cabin)	24	22	91.7%
Total	4601	413	9.0%

	Bats from Mistnets	Shrews from Pitfalls*	Pitfall Nights
Kyoha River	1	1	15
Maahoma River	-	5	10
Nyabitala Camp	5	3	10
Lake Maahoma	-	3	20
John Mate Camp	23	6	15
Lake Bujuku	-	0	15

TABLE II: Daily Capture Rate and Species Diversity for Well Surveyed Camps (bats and carnivores excluded)

	Days	Captures	Avg-Daily Capture	Species Captured
Nyona, 1990	9	146	16.2	14
Kyoha, 1991	7	132	18.9	10
Nyabitala, 1990	11	186	16.9	11
Nyabitala, 1991	8	133	16.6	11

Table III: Activity Patterns of Specimens Collected in 1991

Species	N=	Nocturnal	Diurnal
<i>Cricetomys emini</i>	9	9	-
<i>Crocidura montis</i>	3	1	2
<i>Crocidura mobbe</i>	1	1	-
<i>Crocidura olivieri</i>	5	4	1
<i>Dasymys montanus</i>	8	3	5
<i>Dendrohyrax arboreus</i>	3	2	1
<i>Dendromus insignis</i>	7	7	-
<i>Dendromus kivu</i>	5	5	-
<i>Galerella sanguineus</i>	1	-	1
<i>Genetta servalina</i>	3	2	1
<i>Hybomys lunaris</i>	17	2	15
<i>Hylomyscus denitiae</i>	127	125	2
<i>Lophuromys flavopunctatus</i>	84	36	48
<i>Lophuromys woosnami</i>	14	14	-
<i>Miniopterus inflatus</i>	1	1	-
<i>Mus bufo</i>	42	26	16
<i>Myosorex blarina</i>	3	2	1
<i>Oecomys hypoxanthus</i>	1	1	-
<i>Oecomys denti</i>	4	3	1
<i>Oecomys typus</i>	15	9	6
<i>Praomys jacksoni</i>	78	77	1
<i>Rousettus angolensis</i>	2	2	-
<i>Rousettus lanosus</i>	24	24	-
<i>Sylvisorex granti</i>	12	8	4
<i>Sylvisorex lunaris</i>	4	4	-
<i>Sylvisorex vulcanorum</i>	1	1	-

TABLE IV: Percentage of Sub-Adult/Adult Females with Embryos

Species	1990				1991				
	Ky	Ma	Ny	Total	Ky	Ma	Ny	JM	Bu
<i>Cricetomys emini</i>	0/1	0/3	0/1	0/5	0/3	0/1	0/1	-	0/5
<i>Crocidura dolichura</i>	-	-	-	-	0/1	-	-	-	0/1
<i>Crocidura montis</i>	-	-	-	-	-	-	0/1	0/2	0/3
<i>Crocidura niobe</i>	-	1/4	-	1/4	-	-	-	-	-
<i>Crocidura olivieri</i>	0/1	1/2	0/4	1/7	-	-	1/2	-	1/2
<i>Dasymys montanus</i>	-	-	0/1	0/1	-	-	0/3	-	0/3
<i>Dendrohyrax arboreus</i>	-	-	-	-	-	-	-	0/1	0/1
<i>Dendromus lunaris</i>	-	0/1	-	0/1	-	-	0/2	0/1	0/3
<i>Dendromus insignis</i>	-	-	-	-	-	-	0/1	0/2	0/3
<i>Funisciurus carruthersi</i>	-	-	-	-	1/1	-	-	-	1/1
<i>Graphiurus murinus</i>	-	0/1	-	0/1	-	-	-	-	-
<i>Galerella sanguinea</i>	-	0/1	-	-	-	-	-	-	-
<i>Hylomys lunaris</i>	2/4	0/10	1/1	3/15	1/4	-	-	-	1/4
<i>Hylomyscus denniae</i>	0/2	1/5	9/29	10/36	1/2	1/13	2/20	3/10	2/13
<i>Lophuromys flavopunctatus</i>	0/1	1/3	8/32	9/36	-	0/1	1/15	3/7	1/16
<i>Lophuromys woosnami</i>	2/7	1/9	1/12	4/28	3/3	1/1	0/5	-	4/9
<i>Miniopterus inflatus</i>	-	-	-	-	-	-	-	-	-
<i>Mus bufo</i>	2/9	0/3	0/5	2/17	5/10	-	1/4	-	6/14
<i>Myosorex blarina</i>	0/2	-	-	0/2	-	-	0/1	0/1	0/2
<i>Myotis welwitschii</i>	0/1	-	-	0/1	-	-	-	-	-
<i>Oenomys hypoxanthus</i>	0/1	1/2	-	1/3	-	-	0/1	-	0/1
<i>Otomys denti</i>	-	0/1	0/1	0/2	-	-	0/1	0/1	0/2
<i>Otomys typus</i>	-	-	-	-	-	-	1/3	2/6	3/9
<i>Praomys jacksoni montis</i>	8/22	3/32	-	11/54	9/23	0/3	-	-	9/26
<i>Roussettus angolensis</i>	3/4	9/18	1/5	13/27	-	-	1/1	-	1/1
<i>Roussettus lanosus</i>	-	-	1/3	1/3	-	-	5/17	-	5/17
<i>Sylvioorex granti</i>	-	-	-	-	-	0/1	0/2	0/1	0/4
<i>Sylvioorex lunaris</i>	0/4	-	-	0/4	-	-	0/1	-	0/1
<i>Sylvioorex vulcanorum</i>	0/1	-	-	0/1	-	-	-	-	-

TABLE V: Percentage of Juveniles for Common Species

	By Weight Nov/Dec 1990	By Weight Feb/Mar 1991
<i>Hylomyscus denniae</i>	7/44 = 16%	20/65 = 31%
<i>Mus bufo</i>	11/55 = 20%	6/40 = 15%
<i>Lophuromys flavopunctatus</i>	13/82 = 16%	21/91 = 23%
<i>Lophuromys woosnami</i>	6/58 = 10%	0/13 = 0%
<i>Praomys jacksoni montis</i>	47/131 = 36%	32/73 = 44%

	By Dental Wear Nov/Dec 1990	By Dental Wear Feb/Mar 1991
<i>Hylomyscus denniae</i>	9/45 = 20%	26/65 = 40%
<i>Mus bufo</i>	9/31 = 29%	13/25 = 52%
<i>Lophuromys flavopunctatus</i>	25/57 = 44%	15/46 = 33%
<i>Lophuromys woosnami</i>	10/32 = 31%	0/10 = 0%
<i>Praomys jacksoni montis</i>	37/65 = 57%	39/54 = 72%

Table VI: Diversity as a Function of Elevation
1990 & 1991 Field Seasons Separate

Camp Species	1990				1991					
	Ky	Ma	Ny	Total	Ky	Ma	Ny	LM	JM	Bu
<i>Cricetomys emini</i> ssp.	2	12	2	16	6	2	3	-	-	-
<i>Crocidura dolichurassp.</i>	-	-	-	-	1	-	-	-	-	-
<i>Crocidura montis</i>	-	-	-	-	-	-	-	1	2	-
<i>Crocidura niobe</i>	9	-	-	9	1	-	-	-	-	-
<i>Crocidura olivieri</i> ssp.	1	2	6	9	-	-	5	-	-	-

Table VI cont.

Camp	1990				1991						
	Ky	Ma	Ny	Total	Ky	Ma	Ny	LM	JM	Bu	Total
<i>Dasymys montanus</i>	-	-	2	2	-	-	1	-	7	-	8
<i>Dendrohyrax arboreus</i> ssp.	-	1	-	1	-	-	-	-	-	-	3
<i>Dendromys kivu</i>	-	1	-	1	-	-	-	-	1	2	10
<i>Dendromys insignis</i> ssp.	-	-	-	-	-	-	-	-	4	3	7
<i>Funisciurus carruthersi</i> ssp.	-	-	-	-	2	-	-	-	-	-	2
<i>Genetta servalina</i> ssp.	-	-	-	-	1	1	1	-	-	-	3
<i>Graphiurus murinus</i> ssp.	-	4	-	4	-	-	-	-	-	-	1
<i>Herpestes sanguineus</i> ssp.	-	1	-	1	-	1	-	-	-	-	1
<i>Hybomys lunaris</i>	7	22	6	35	17	1	-	-	-	-	18
<i>Hylomyscus d. denniae</i>	6	13	54	73	5	-	61	2	27	33	128
<i>Lophuromys flavopunctatus</i> ssp.	4	7	73	84	2	2	32	5	17	32	90
<i>Lophuromys w. woosnami</i>	12	23	23	58	3	2	6	6	-	-	17
<i>Miniopterus inflatus</i>	-	1	-	1	-	-	-	-	-	-	0
<i>Mus b. bufo</i>	36	13	15	64	24	1	18	1	-	-	44
<i>Myosorex blarina</i>	4	-	-	4	-	-	-	-	-	-	3
<i>Myotis welwitschii venustus</i>	1	-	-	1	-	-	-	2	-	1	1
<i>Oenomys hypoxanthus</i> ssp.	1	5	-	6	-	-	1	-	-	-	4
<i>Otomys d. denti</i>	-	1	2	3	1	-	-	-	2	1	16
<i>Otomys typus dartmouthi</i>	-	-	-	-	-	-	-	-	5	11	1
<i>Pipistrellus kuhlii fuscatus</i>	-	-	-	-	-	-	1	-	-	-	78
<i>Praomys jacksoni</i> c.f. <i>montis</i>	57	80	-	137	69	9	-	-	-	-	2
<i>Rhinolophus m. ruwenzorii</i>	-	1	1	2	-	-	2	-	-	-	2
<i>Rousettus a. ruwenzorii</i>	4	29	4	37	1	-	1	-	-	-	2
<i>Rousettus l. lanosus</i>	1	-	3	4	-	-	1	-	23	-	24
<i>Sylvisorex g. granti</i>	1	-	2	3	-	3	3	2	4	1	13
<i>Sylvisorex l. lunaris</i>	5	-	-	5	-	1	1	-	-	-	4
<i>Sylvisorex vulcanorum</i>	1	1	1	3	-	-	-	-	-	-	1

Table VII: Diversity as a Function of Elevation
1990 & 1991 Field Seasons Combined

Camp	INSECTIVORA						Ky	Ma	Ny	LM	JM	Bu	Total
	<i>Crocidura dolichura</i> ssp.	1	-	-	-	-	-	-	-	-	-	-	1
	<i>Crocidura montis</i>	-	-	-	-	-	-	-	1	2	-	-	3
	<i>Crocidura nioke</i>	10	-	-	-	-	-	-	-	-	-	-	10
	<i>Crocidura oliveri</i> ssp.	1	2	11	-	-	-	-	-	-	-	-	14
	<i>Myosorex blarina</i>	4	-	-	-	-	-	-	2	1	1	7	7
	<i>Sylvisorex granti granti</i>	1	3	5	2	4	1	1	2	4	1	16	16
	<i>Sylvisorex lunaris lunaris</i>	5	1	1	1	2	-	-	-	-	-	9	9
	<i>Sylvisorex vulcanorum</i>	1	2	2	-	-	-	-	-	-	-	5	5
	CHIROPTERA												
	<i>Rousettus angolensis ruwenzorii</i>	5	29	5	-	-	-	-	-	-	-	39	39
	<i>Rousettus lanosus lanosus</i>	1	-	4	-	-	23	-	-	-	-	28	28
	<i>Rhinolophus macclaudi ruwenzorii</i>	-	1	3	-	-	-	-	-	-	-	4	4
	<i>Miniopterus inflatus</i>	-	1	-	-	-	-	-	-	-	-	1	1
	<i>Myotis welwitschii venustus</i>	1	-	-	-	-	-	-	-	-	-	1	1
	<i>Pipistrellus kuhlii fuscatus</i>	-	-	1	-	-	-	-	-	-	-	1	1
	CARNIVORA												
	<i>Genetta servalina</i> ssp.	1	1	1	-	-	-	-	-	-	-	3	3
	<i>Galerella sanguineus</i> ssp.	-	2	-	-	-	-	-	-	-	-	2	2
	HYRACOIDEA												
	<i>Dendrohyrax arboreus</i> ssp.	-	1*	-	-	-	2	2	2	2	5	5	5
	RODENTIA												
	<i>Funisciurus carruthersi</i> ssp.	2	-	-	-	-	-	-	-	-	-	2	2
	<i>Cricetomys emini</i> ssp.	8	14	5	-	-	-	-	-	-	-	27	27
	<i>Dendromus kivu</i> ssp.	-	1	-	-	-	7	3	3	11	11	11	11
	<i>Dendromus insignis pectivali</i>	-	-	-	-	-	4	2	2	7	7	7	7
	<i>Dasymys montanus</i>	-	-	3	-	-	7	-	-	10	10	10	10
	<i>Hybomys lunaris</i>	24	23	6	-	-	-	-	-	-	-	53	53
	<i>Hylomyscus d. denniae</i>	11	13	115	2	27	20	20	20	201	201	201	201
	<i>Lophuromys flavopunctatus</i> ssp.	6	9	105	5	17	25	25	25	174	174	174	174
	<i>Lophuromys woosnami</i> ssp.	15	25	29	6	-	-	-	-	75	75	75	75
	<i>Mus bufo</i> ssp.	60	14	33	1	-	-	-	-	108	108	108	108
	<i>Oenomys hypoxanthus</i> ssp.	1	5	1	-	-	-	-	-	7	7	7	7
	<i>Praomys jacksoni montis</i>	126	89	-	-	-	-	-	-	215	215	215	215
	<i>Otomys denti denti</i>	1	1	2	-	-	2	1	1	7	7	7	7
	<i>Otomys typus dartmouthi</i>	1	-	-	-	-	5	11	11	16	16	16	16
	<i>Graphiurus murinus</i> ssp.	-	4	-	-	-	-	-	-	4	4	4	4
	TOTAL RODENTIA	254	198	299	14	69	63	63	63	917	917	917	917

Table VIII: Small Mammals known from the Ugandan Slope of Rwenzori and their Elevational Range

vegetation type	Grass		Forest		B'boo	Heath	S'cio
	beginning at (m)	1500	Low	High	2600	3300	3800
INSECTIVORA							
<i>Chrysocolotis s. stuhlmanni</i>	-	B	B	B	B	-	-
<i>Crocidura dolichura</i> ssp.	-	F	-	-	F	B	-
<i>Crocidura montis</i> ¹	-	-	-	-	-	-	-
<i>Crocidura niohe</i>	B?	BF	BF	-	-	-	-
<i>Crocidura oliveri nyassae</i>	B?	BF	BF	BF	-	-	-
<i>Myosorex blarina</i> (R)	-	F	F	-	F	F	F
<i>Sylvioorex g. granti</i>	-	F	F	BF	F	F	F
<i>Sylvioorex l. lunaris</i>	B?	BF	BF	B	B	B	B
<i>Sylvioorex vulcanorum</i>	-	F	F	-	-	-	-
CHIROPTERA							
<i>Epomophorus labiatus anurus</i>	B	-	-	-	-	-	-
<i>Rousettus angolensis ruwenzorii</i>	B	BF	F	F	BF	B	-
<i>Rousettus lanosus lanosus</i>	-	F	F	-	-	-	-
<i>Rhinolophus maculadi ruwenzorii</i>	-	F	F	-	-	-	-
<i>Nycteris hispida</i> ssp.	B	-	-	-	-	-	-
<i>Miniopterus inflatus</i> ssp.	-	F	-	-	-	-	-
<i>Myotis welwitschii venustus</i>	-	F	-	-	-	-	-
<i>Pipistrellus nanus</i> ssp.	B	-	-	-	-	-	-
<i>Pipistrellus kuhlii fuscatus</i>	-	-	F	-	-	-	-
CARNIVORA							
<i>Nandinia binotata</i> ssp.	B	-	-	-	-	-	-
<i>Genetta maculata</i> ssp.	B?	B	-	-	-	-	-
<i>Genetta servalina</i> ssp.	-	BF	BF	-	-	-	-
<i>Genetta servalina</i> ssp.	R	RF	-	-	-	-	-
<i>Mungos mungo</i> ssp.	B	-	-	-	-	-	-
RODENTIA							
<i>Paraxerus boehmi emini</i>	B?	B	-	-	-	-	-
<i>Funisciurus cauruthersi</i> ssp.	-	BF	-	-	-	-	-
<i>Helosciurus ruwenzorii</i> ssp.	-	B	B	-	-	-	-
<i>Cricetomys emini</i> ssp.	B?	BF	F	-	-	-	-
<i>Dendromus insignis percivali</i>	-	-	-	B	F	F	F
<i>Dendromus kivu</i> ssp.	-	F	-	-	-	-	-
<i>Arvicanthus niloticus</i> ssp.	B	-	-	-	-	-	-
<i>Dasymys incomtus</i> ssp.	B?	B	B	-	-	-	-
<i>Dasymys montanus</i> (R)	-	-	F	-	BF	B	-
<i>Grammomys dryas</i>	B	B	-	-	-	-	-
<i>Hybomys lunaris</i> (R)	B?	BF	F	-	-	-	-

(cont. next page)

Table VIII (cont.): Small Mammals known from the Ugandan Slope of Rwenzori and their Elevational Range

vegetation type	Grass		Forest		B'boo	Heath	S'cio
	beginning at (m)	1500	Low	High	2600	3300	3800
RODENTIA (cont.)							
<i>Hyomyscus d. denimae</i> (R)	B?	BF	BF	BF	BF	BF	BF
<i>Lemiscomys striatus</i> ssp.	B	B	-	-	-	-	-
<i>Lophuromys flavopunctatus</i> ssp.	B?	BF	BF	BF	BF	BF	BF
<i>Lophuromys woosnamii</i> ssp.	B?	BF	BF	BF	-	-	-
<i>Mastomys hildebrandtii</i> ssp.	B?	B	-	-	-	-	-
<i>Mus barto</i> ssp.	B?	BF	BF	F	F	-	-
<i>Mus musculoides gylra</i>	B?	B	-	-	-	-	-
<i>Mus triton fons</i> (NE Rwenzori)	-	B	-	-	-	-	-
<i>Oenomys hypoxanthus</i> ssp.	B?	BF	BF	F	-	-	-
<i>Prionomys jacksoni montis</i> (R)	B?	BF	-	-	-	-	-
<i>Thomomys venustus</i> ssp.	-	-	B	-	-	-	-
<i>Otomys d. denti</i>	B?	BF	F	B	F	F	F
<i>Otomys typus dartmouthi</i>	-	-	-	-	-	-	-
<i>Graphiurus murinus</i> ssp.	B	B?	-	-	BF	BF	BF
Total Number of Species²							
Total Number Endemics	?	33	21	11	13	12	12
% Endemics	?	17	13	9	10	9	9
Bolface = Albertine Rift Endemic		52%	62%	82%	77%	75%	
(R) = Rwenzori Endemic							

F = Field Museum/Nakerere Expedition
B = British Museum Expedition

B? = see Methods

¹ = also known from Mt. Meru and Imatong Mts., Demeter and Hutterer 1986
² - Carnivora excluded

Table IX: Distribution of Rwenzori Small Mammals by Guild and Elevation

camp elevation	Ky 1920m	Ma 2100m	Ny 2650m	JM 3350m	Bu 3900m
FOREST ZONE FALLOUT					
<i>Funisciurus carnubersi</i>	<1%	-	-	-	-
<i>Graphiurus murinus</i>	-	2%	-	-	-
<i>Cricetomys emini</i>	3%	7%	2%	-	-
<i>Lophuromys woosnamii</i>	6%	13%	10%	-	-
<i>Mus bufo</i>	24%	7%	11%	-	-
<i>Oenomys hypoxanthus</i>	<1%	3%	<1%	-	-
	34%	32%	24%		
STENOCEPHALIC GUILDS					
Grass-Seed Eaters					
<i>Dendromus insignis</i>	-	-	-	6%	5%
<i>Dendromus kivu</i>	-	<1%	-	10%	5%
Grazers					
<i>Dasymys montanus</i>	-	-	1%	10%	0%
<i>Otomys denti</i>	<1%	<1%	<1%	3%	2%
<i>Otomys typus</i>	-	-	-	7%	17%
				36%	29%
DIURNAL DISPLACEMENT					
<i>Hybomys lunaris</i>	9%	12%	2%	-	-
<i>Lophuromys flavopunctatus</i>	2%	5%	35%	25%	40%*
DOMINANT NOCTURNAL MURINES					
<i>Hybomys d. denimae</i>	4%	7%	38%	39%	32%*
<i>Praomys jacksoni montis</i>	50%	45%	-	-	-
Total Rodents	99%	101%	100%	100%	101%

*does not include 13 H. denimae and 7 L. flavopunctatus captures within Bujuku Hut

ROOST COEFFICIENTS (% of all fruit hosts captured)

<i>Rousettus angolensis</i>	7%	43%	7%	-	-
<i>Rousettus lanosus</i>	1%	-	6%	34%	-

TABLE X: Mammal Taxa Described from the Rwenzori: 1894-1997

Taxon Named	Current Status	Author	Year
<i>Potamogeton rwenzori</i>	<i>Micropotamogeton rwenzori</i>	de Witte & Frechkop	1955
<i>Chrysocloris stuhlmanni</i>	<i>Chrysocloris stuhlmanni</i>	Matschie	1894
<i>Crocidura fumosa montis</i>	<i>Crocidura montis</i>	Thomas	1906
<i>Crocidura niobe</i>	<i>Crocidura niobe</i>	Thomas	1906
<i>Myosorex blarina</i>	<i>Myosorex blarina</i>	Thomas	1906
<i>Sylvisorex granti</i>	<i>Sylvisorex granti</i>	Thomas	1906
<i>Sylvisorex lunaris</i>	<i>Sylvisorex lunaris</i>	Thomas	1907
<i>Sylvisorex suncoides</i>	<i>Ruwendivorex suncoides</i>	Thomas	1906
<i>Rousettus angolensis rwenzori</i>	<i>R. a. rwenzori</i>	Osgood	1936
<i>Rousettus lanosus</i>	<i>Rousettus lanosus</i>	Eisenbraun	1965
<i>Rhinolophus rwenzori</i>	<i>R. macclaudi rwenzori</i>	Thomas	1906
<i>Cercopithecus stuhlmanni carnubersi</i>	<i>Cercopithecus mitis</i>	Hill	1942
<i>Colobus rwenzori</i>	<i>Colobus angolensis</i>	Pocock	1907
<i>Crossarchus fasciatus macrurus</i>	<i>Mungos mungo</i>	Thomas	1907
<i>Mungos gracilis proteus</i>	<i>Galerella sanguinea</i>	Thomas	1907
<i>Felis pardus rwenzori</i>	<i>Panthera pardus</i>	Thomas	1907
<i>Procavia (Dendrohyrax) rwenzori</i>	<i>Dendrohyrax arboreus</i>	Canerano	1906
<i>Cephalophus rubidus</i>	<i>Cephalophus rubidus</i>	Neumann	1906
<i>Funisciurus carnubersi</i>	<i>F. carnubersi</i>	Thomas	1902
<i>Sciurus rubrobrachiatatus rwenzori</i>	<i>Heliosciurus rwenzori</i>	Thomas	1906
<i>Dendromus lunaris</i>	<i>Dendromus kivu</i>	Schwann	1904
<i>Tatera rwenzori</i>	<i>Tatera valida</i>	Osgood	1936
<i>Dasymys medius</i>	<i>Dasymys incontinens medius</i>	Thomas & Wroughton	1910
<i>Dasymys montanus</i>	<i>Dasymys montanus</i>	Thomas	1906
<i>Leggada bufo</i>	<i>Mus bufo</i>	Thomas	1906
<i>Leggada fors</i>	<i>Mus triton</i>	Thomas & Wroughton	1906
<i>Leggada grata</i>	<i>Mus musculoides</i>	Thomas & Wroughton	1910
<i>Avicannulus maculatus</i>	<i>Lemniscomys maculatus</i>	Thomas & Wroughton	1910
<i>Funisciurus woosnamii</i>	<i>L. woosnamii</i>	Thomas & Wroughton	1910
<i>Mus denimae</i>	<i>Hybomyscus denimae</i>	Thomas	1906
<i>Mus univittatus lunaris</i>	<i>Hybomys lunaris</i>	Thomas	1906
<i>Mus jacksoni montis</i>	<i>Praomys montis</i>	Thomas	1906
<i>Oenomys baechante edulis</i>	<i>Oenomys hypoxanthus</i>	Thomas & Wroughton	1910
<i>Thamnomys dryas</i>	<i>Grammomys dryas</i>	Thomas & Wroughton	1910
<i>Thamnomys venustus</i>	<i>Thamnomys venustus</i>	Thomas	1907
<i>Otomys dartrouthi</i>	<i>Otomys typus dartrouthi</i>	Thomas	1907
<i>Otomys denti</i>	<i>Otomys denti</i>	Thomas	1906
<i>Graphiurus soleatus</i>	<i>Graphiurus murinus</i>	Thomas & Wroughton	1906

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Appendix: Notes on the Collection of Voucher Specimens

1) Conservation efforts should prioritize the maintenance of ecosystems rather than individual organisms. Collections, and the publications based on them, will establish a baseline so that future monitoring efforts have a reference for comparison.

2) Vouchers must be deposited in maintained museums and herbaria both in Uganda and elsewhere. In this way, specimens are available for review by scientists in order to resolve discussions over taxonomic status. Such accredited institutions are designed to care for these irreplaceable specimens.

3) We must be able to identify that which we are attempting to conserve. For small mammals and most other organisms, this requires the collection of specimens. Most organisms cannot be identified without voucher specimens. Identification in the hand is often impossible. For small mammals we depend upon skins, skulls, teeth, ectoparasites, DNA, chromosomes, genitalia, bacula, soft anatomy, etc.; often requiring the sacrifice of the animal. The three most speciose mammalian groups are shrews (428), bats (925) and rodents (2021); one African shrew genus, *Crocidura*, alone contains 149 species (Wilson and Reeder 1992). These three groups comprise 73% of mammalian diversity and many species cannot be properly identified in the field.

4) Among small mammal identification keys, the best available (e.g. Delany, 1975; Meester & Setzer, 1972) are terribly out-of-date and are, at best, good to the level of genus only. Further, these keys can only be used when a clean skull is available. Collections, such as ours, will help to construct keys with greater resolution.

5) Large series of specimens are often required to resolve species identifications. For example, in this Rwenzori survey, 201 individuals of *Hylomyscus demissa demissa* were collected from all 7 sites. Of these, only 28 were fully grown adult males (dentate stage 5 and above, Verheyen and Bracke 1966). This sample of 28 barely allowed us to demonstrate that this species did not vary with elevation. Using these data, we can demonstrate that much smaller specimens, previously referred to as "*Hylomyscus demissa*" from Mgahinga Gorilla National Park, are really a distinct taxon known as "*Hylomyscus demissa vulcanorum*", described from the Virungas in 1925 (Lombard and Gyldestolpe). This also means that *Hylomyscus demissa demissa* may only be known from the Rwenzori.

6) Scientific methodology requires the collection of vouchers. Data must be verifiable, refutable and subject to further analyses. For example, the first worldwide mammal checklist (Honacki et al., 1974) listed 433 species of mice versus the most recent checklist (Wilson & Reeder, 1992) which lists 529, an increase of 22%. However, most of these are not newly described species. Of the total of 460 new mammal taxa recognized in this 18 year period, 290 (63%) were resurrected from synonymy (meaning from previously described specimens residing in museums). This reflects our changing perceptions of species definitions as well as the increasing number of tools available to discriminate closely related taxa (DNA, chromosomes, multivariate statistics, etc.).

7) We use the standard Species Accumulation Curve in determining whether we have accurately documented the fauna of a given camp. Numbers of new species encountered each day are plotted against cumulative trap effort (e.g. trapnights). When the curve reaches a plateau, and no new species are encountered for several days, we

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assume that we have documented most of the mammal species targeted by our methodology. Invariably, species that are the most common or abundant are encountered first and in the highest numbers. Only after the removal of the more common species are less frequent species observed. The number of camps is chosen to sample the maximum number of ecological zones within the protected area. These zones are typically determined by elevational range, edaphic conditions and vegetation communities.

8) After a particular protected area is properly surveyed for small mammals, specimens are distributed to the appropriate institutions and alpha-taxonomists. Identification keys can then be developed in order to identify the relevant species in the hand. At this point, ecological studies can begin. However, even at this point, severely flawed. For example, numerous South African studies of *Mastomys natalensis* which species was the subject of the dozens of ecological, behavioral, and medical studies which were conducted (Meester, 1990).

9) Our methodologies have minimal impact on communities of small mammals. Small mammals, especially rodents, have exceptionally high reproductive turnover. The Makerere University/Field Museum Rwenzori expedition of 1990/1991 gathered 1039 rodents, shrews and bats from 6 camps along a single transect. This number of small mammals would be consumed by a single owl (actually 1.15 owls) over the same three month time period (assuming a daily capture rate of 10 rodents; Yates, et al. 1987).

Daniel Aleper (1995) provided relevant data from Bwindi-Impenetrable National Park. In his one hectare open-canopy study plot, small mammal numbers increased from 31 to 73 individuals during a three month period. This translates into a 1 1/2 million increase in the small mammal population for the 331 km² park during this period. This is an underestimate, including accurate population estimates for shrews, bats and larger rodents might double these figures. The removal of several hundred small mammals from different localities in Bwindi would have a negligible impact.

In order to have an indication of small mammal density and to understand the level of trapping intensity, we present trapnight data from the 1991 field season (Table 1). Although we do not have data on trap success for our first expedition, it is worth noting that trap success in 1991 is quite high for Kyoha and Nyabataba (averaging 10%), only five months after the first expedition. Sites unsampled in 1990 (John Male and Lake Buyuku) have relatively low trap success (5.5% and 8.4%) but this may simply reflect differing small mammal densities in the different habitats.

Assuming similar trapping effort between the two field seasons, a comparable number of specimens were recovered on a daily basis from the two intensively surveyed camps (Table II): Kyoha, approx. 16 specimens per day in 1990 vs. 19 in 1991; Nyabataba, approx. 17 specimens per day in both 1990 and 1991. Available data do not suggest a depletion of small mammal numbers from one field season to the next. This suggests that our trapping efforts have little effect on small mammal demographics and, in fact, that other variables are far more influential in affecting small mammal populations.