Rodents of the afro-alpine zone of Mt. Elgon

Viola Clausnitzer

Introduction

"The mountains are Africa's Galápagos Islands" (KINGDON, 1989). The flora and fauna of these montane islands differ from the surrounding lowlands, bearing a number of endemics and species with highly disjoint distribution, as well as having developed a number of unique life forms. Some of these conspicuous elements can be found on virtually all of the East African mountains. Although montane forests formed a migration belt in the last ice age, no evidence for continuous afro-alpine environments was found so far (HAMILTON, 1982).

The isolated mountains in East Africa have never attracted the same degree of scientific attention as their neighbouring savanna biomes. Few studies on the afro-alpine rodent communities have been carried out, e.g. in the Simien Mts., focusing on the population ecology of *Arvicanthis abyssinicus* (MÜLLER, 1977). This report will concentrate on the four most common species in the afro-alpine grasslands of Mt. Elgon: *Rhabdomys pumilio, Lophuromys flavopunctatus, Otomys barbouri* and *O. typus.*

Taxonomic note

Nomenclature follows MUSSER and CARLETON (1993), except for the Mt. Elgon endemic *Otomys barbouri.* This species was described by LAWRENCE and LOVERIDGE (1953), later considered as a subspecies of *O. anchietae* and only recently rehabilitated

(DIETERLEN and VAN DER STRAETEN, 1992), a position followed by TAYLOR and KUMIRAI (2001).

Study site

Mt. Elgon (4321 m a.s.l.) is an isolated massif of volcanic origin straddling the Kenya-Uganda border (0°54'-1°25'N and 34°14'-34°45'E), which was deglaciated about 12000 years BP. The volcano rises from a plateau lying at 1850-2000 m a.s.l. to the east and 1050 - 1350 m a.s.l. to the west; the longest north-south distance is about 80 km, the longest east-west distance 50 km.

The montane vegetation and the extension of the different vegetation belts are influenced for long by human impacts, e.g. grazing and burning, and by climate degradation. Moorlands and tussock-grasslands extend down to 3200 m a.s.l. due to frequent burning. Ericaceous forest is only found in small patches and along valleys. Downwards, *Hagenia* and *Rapanea* forests are mixed with bamboo patches terminating in montane forest.

The study sites were situated on the western slopes of Mt. Elgon, between 3650 and 3800 m a.s.l., near the Dirigana Valley. During the study period the precipitation at that elevation was 911 mm per year, April and September were the wettest months, and the average temperature was 5,4° C.

Methods

Three 1 ha grids were laid out for a mark-recapture study. Each of these grids consisted of 11 parallel lines, 10 m apart. The lines had trapping stations with two traps every 10 m, resulting in 121 trapping stations and 242 traps per grid. Trapping was done with Sherman live traps (Large and Extra Large) baited with a peanut-cassava flour mixture for four days each month from October 1996 to November 1997. Since the *Otomys* species were not attracted by any bait the traps were placed directly in their surface runway system. The difficulties in catching *Otomys* were described before by various authors (e.g. KINGDON, 1974; SHORE and GARBETT, 1991).

Additionally rodents were surveyed along an elevation gradient on the western side of Mt. Elgon. The transect covered representative vegetation formations of different altitudes between 2900 and 4200 m a.s.l. Sampling was done for two consecutive nights every two month between October 1996 and October 1997. The traps were placed in three trap-lines (N-S direction) 40 m apart. Trap stations were set at 20-m intervals with one small and one large break-back trap baited with a peanut-cassava-oil mixture. The traps were laid in surface runways if possible, to increase the trapping success for *Otomys*. Voucher specimens from this study are deposited in the Naturkunde Museum Schloß Rosenstein, Stuttgart, Museum Alexander Koenig, Bonn and the Zoology Museum of the Makerere University, Kampala.

The animals from the mark-recapture grids were individually marked by toe-clipping, weighed to the nearest gram, measured and the sexual condition and ectoparasites were recorded. The vegetation was mapped for all three grids, the vertical structure measured using the point-intercept method; all plants were identified (WESCHE, 2000). Invertebrates were trapped with six pitfalls at the same time as each trapping session on the mark-recapture grids, weighed and identified at least to the order.

Faeces of individuals of *Otomys barbouri* and *O. typus* were collected on the mark-recapture grids from the traps and later analysed using a microscope. For identification of the cell fragments in the pellets a cell catalogue was prepared from sampled plant species. Some of the cell fragments could be identified up to species level. The diet of *Lophuromys flavopunctatus* was analysed from the stomachs of animals caught in the trap-lines.

Individuals of *Otomys typus* and *O. barbouri* were radio-tracked for several days, using a TRX-10002 receiver (Widlife Materials, Canada) and MD-2C transmitters (Holohil Systems, Canada).

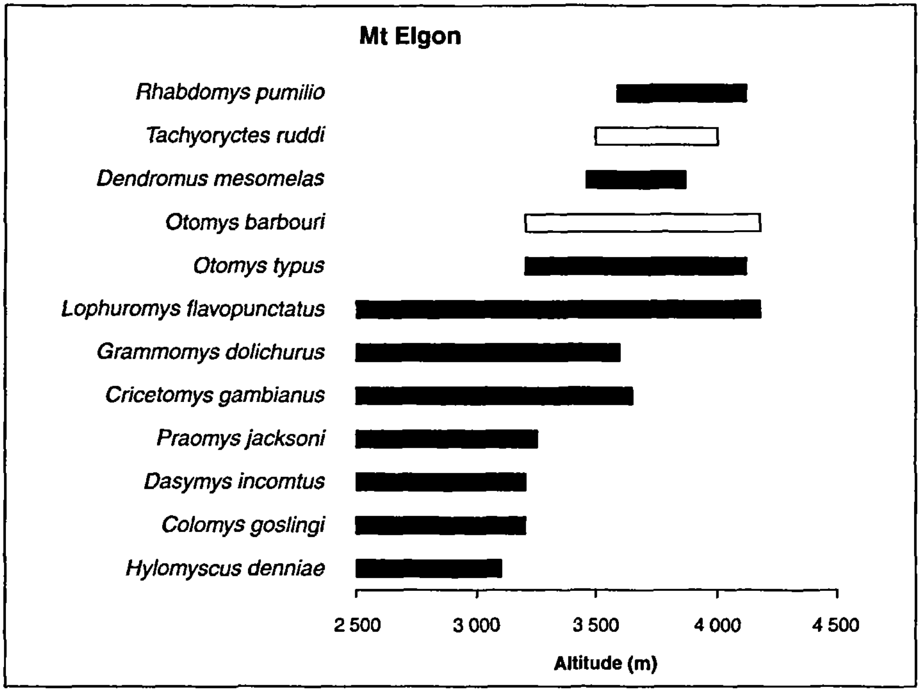


Figure 1
Vertical distribution of rodents on the western slopes of Mt. Elgon; white bars indicate endemics.

Results and discussion with notes on selected species

A total of 384 rodents consisting of 13 species were caught in 4200 trap-nights. A clear change in species composition on Mt. Elgon occurs at about 3200 m a.s.l., which coincides with the present upper limit of the montane forest (fig. 1).

Endemic rodents are only found in the afro-alpine zone, where they inhabit ericaceous vegetation, moorlands and tussock grasslands ranging between 3300 - 4300 m a.s.l. The moorlands and tussock-grasslands above 3700 m a.s.l. on Mt. Elgon are permanently inhabited by 9 rodent species, 8 of them belonging to the Muridae (table 1).

MURIDAE	
Cricetomys gambianus Waterhouse, 1840	
Dendromus mesomelas (Brants, 1827)	X
Grammomys dolichurus (Smuts, 1832)	
Lophuromys flavopunctatus Thomas, 1888	X
Otomys barbouri Lawrence and Loveridge, 1953	X
Otomys typus Heuglin, 1877	X
Rhabdomys pumilio (Sparrman, 1784)	X
Tachyoryctes ruddi Thomas, 1909	X
GLIRIDAE	
Graphiurus murinus (Desmarest, 1822)	

Table 1
Rodents of Mt. Elgon above 3700 m a.s.l.; the most common ones are underlined; x: abundant in grassland habitats.

Lophuromys flavopunctatus *Thomas, 1888*

Lophuromys flavopunctatus is one of the most numerous rodents in the moister areas of East Africa, inhabiting a wide range of different habitats over a large geographical zone. For example in the Ruwenzori Mts. it occurs from lowland forests at about 500 m a.s.l. to the afro-alpine zone reaching well above 4200 m a.s.l. (MISONNE, 1963). Its opportunistic abilities to colonize also less favourable habitats, e.g. the ericaceous belt and montane moorlands, makes *L. flavopunctatus* one of the most successful rodents (MISONNE, 1969).

Lophuromys flavopunctatus has specialized on invertebrates and vertebrates (e.g. small frogs) and is highly dependent on this protein rich diet. HANNEY (1964) reported that *L. flavopunctatus* kept in captivity would not survive for over a week unless fed with worms, frogs or insects. DIETERLEN (1976) could keep individuals on a meat-free diet for several months, feeding them with nuts and sun-flower seeds, but such animals would loose weight drastically and would not reproduce. Compared to mainly vegetarian rodents, the time *Lophuromys* species spend feeding is very short (KINGDON, 1974). In many rodent communities representatives of the genus *Lophuromys* are the only entomophagous species (e.g. VERSCHUREN *et al.*, 1983).

The food particles found in stomachs of *Lophuromys flavopunctatus* belonged largely to the following categories: 1. invertebrates, 2. plant material, and 3. mosses. Vertebrates were not considered since these were most often snap-trapped conspecifics, nor were roots and earth, occasionally found in the stomachs and probably ingested accidentally while searching for and consuming soil-dwelling invertebrates.

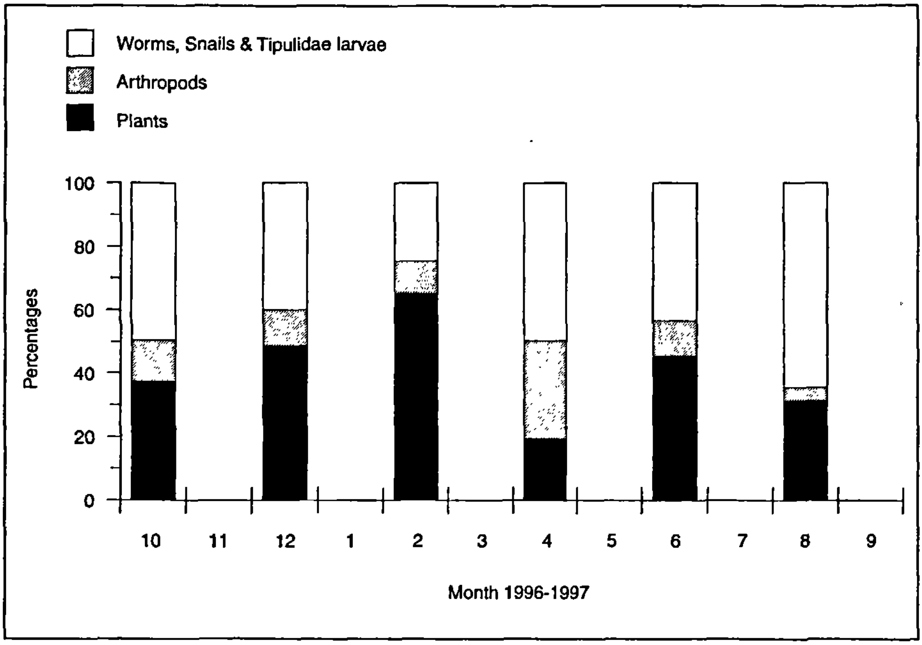


Figure 2
Seasonal changes in the diet of *Lophuromys flavopunctatus*.

Vascular plants were mainly parts of monocotyledons, with only few dicotyledons. A part of them may also have been ingested accidentally with invertebrates.

Figure 2 shows the seasonal changes in the diet of *Lophuromys flavopunctatus* caught in afro-alpine grasslands 3800 m a.s.l. The major food items are soil-dwelling invertebrates, namely earthworms, snails, and insect larvae (Tipulidae). Plants are also a food source, but not necessarily the first choice. In the driest month, February, the plant proportion reached a maximum with over 50%. In April and August, the wettest months, the stomachs contained the highest invertebrate portion, mainly earthworms and *Tipula* larvae. These subterranean invertebrates are rare and difficult to get in the dry season. The total weight of invertebrates from the pitfalls correlates significantly with rainfall (fig. 3), (Mann-Whitney U Test; $n_{weight} = 12$; $n_{prec.} = 12$; one-tailed $p = 0.0002$).

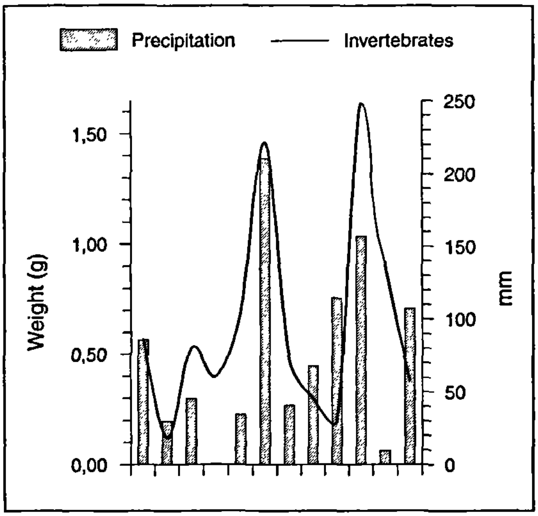


Figure 3
Correlation of the total weight of invertebrates from pitfalls and the monthly precipitation.

Similar positive correlations between the consumption of insects and rainfall have been observed for some rodent species in Africa, e.g. *Rhabdomys pumilio* in South Africa (PERRIN, 1980), *Lemniscomys striatus* in Uganda (FIELD, 1975), *Arvicanthis niloticus* in Kenya (TAYLOR and GREEN, 1976) and *Mastomys natalensis* in Tanzania (LEIRS, 1995).

Otomys barbouri *Lawrence and Loveridge, 1953 and* O. typus *Heuglin, 1877*

Species belonging to the genus *Otomys* were widespread and common in grassland biomes in Africa during the Plio-Pleistocene (DENYS and JAEGER, 1986; DENYS, 1989). Fossils of the whole subfamily Otomyinae predominate in southern African Pleistocene deposits (BRONNER *et al.*, 1988). The present distribution of *Otomys* is disjoint, mainly restricted to montane habitats in tropical Africa and to South African grasslands. This distribution pattern seems to be the result of climatic changes and competition with Murinae, which invaded Africa in the early Pliocene (DENYS and JAEGER, 1986; DENYS, 1989).

Otomys typus and *O. barbouri* are the most common rodents in the afro-alpine zone of Mt. Elgon. They have been recorded at densities

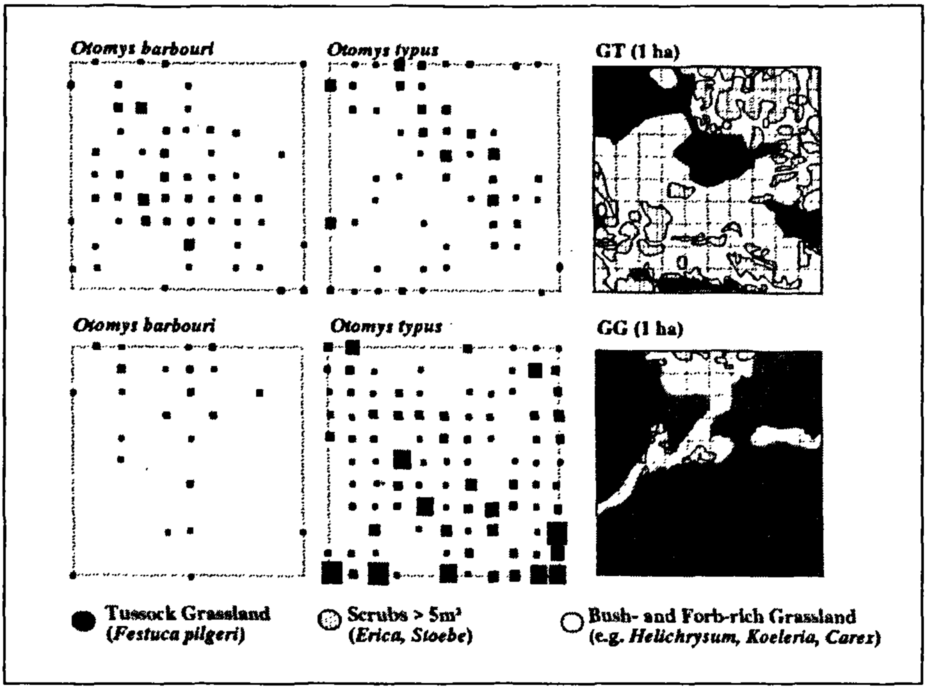


Figure 4
Comparison of two trapping grids, upper line at 3650 m elevation, lower line at 3750 m. Black squares symbolize numbers of individuals of a given species caught at a trap station. Data for a full year summarized. Drawings on the right indicate the corresponding vegetation structure.

of 32 (*O. typus*) and 23 (*O. barbouri*) individuals per hectare, making up a biomass of 3,200 and 2,200 g per ha, respectively.

A total number of 87 *O. barbouri* and of 177 *O. typus* were marked individually on the three grids. The overall recapture rates were 67% for *O. barbouri* and 72% for *O. typus*. In the second half of the study the proportion of recaptured animals in each monthly capture session was at least 80%.

Microhabitat use

Both *Otomys* species coexist sympatrically in large areas on Mt. Elgon, but they show significant differences in their microhabitat use

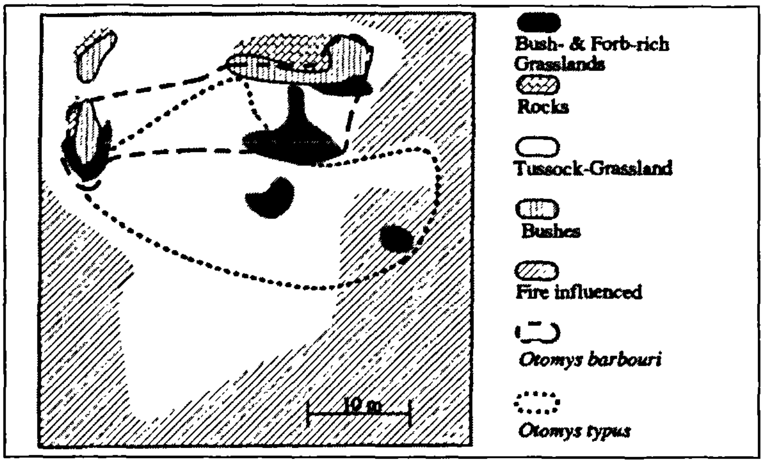


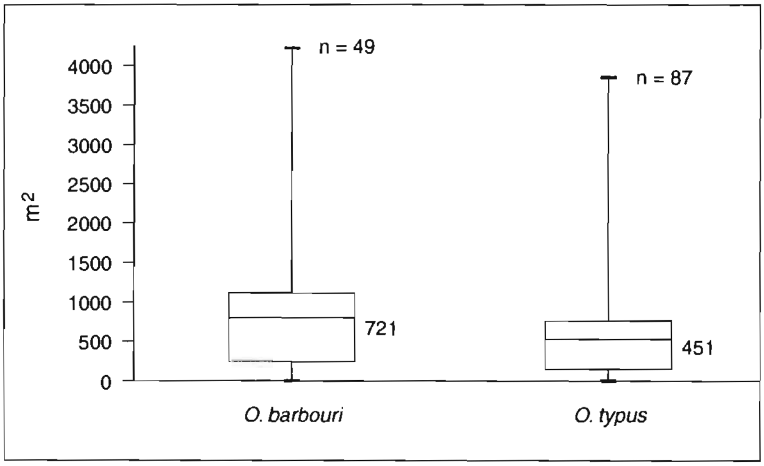
Figure 5
Home range sizes for *Otomys barbouri* and *O. typus* based on a one year mark-recapture study at about 3700 m a.s.l. on Mt. Elgon (100% convex polygons).

(fig. 4). The local distribution of each species depends on vegetation composition and structure and plant species richness. The distribution of *O. barbouri* on structured and species-rich grasslands and of *O. typus* on *Festuca pilgeri*-dominated tussock grasslands was significant (χ2-test: n = 53, p = 0.018).

Figure 4 compares the abundance (on trapping grids) of the Elgon endemic *O. barbouri* with that of the more widely distributed *O. typus*, in relation with vegetation structure. *Otomys barbouri* prefers patchy grasslands or those rich in shrubs, whereas pure tussocks are avoided. In contrast, *O. typus* avoids patchy vegetation and prefers tussock grasslands. Dense scrub is inhabited by none of the species. The lower grid is a much more uniform grassland where the endemic species is rare, whereas *O. typus* is abundant. The relatively small home ranges, as calculated with the 100% convex polygon method (fig. 5), make such microhabitat analysis sensible. The home-range sizes for both species did not vary between males and females.

Figure 6 illustrates the habitat preferences of the 2 *Otomys* species on Mt. Elgon. Radio-tracked *O. typus* (n = 4) moved only within the

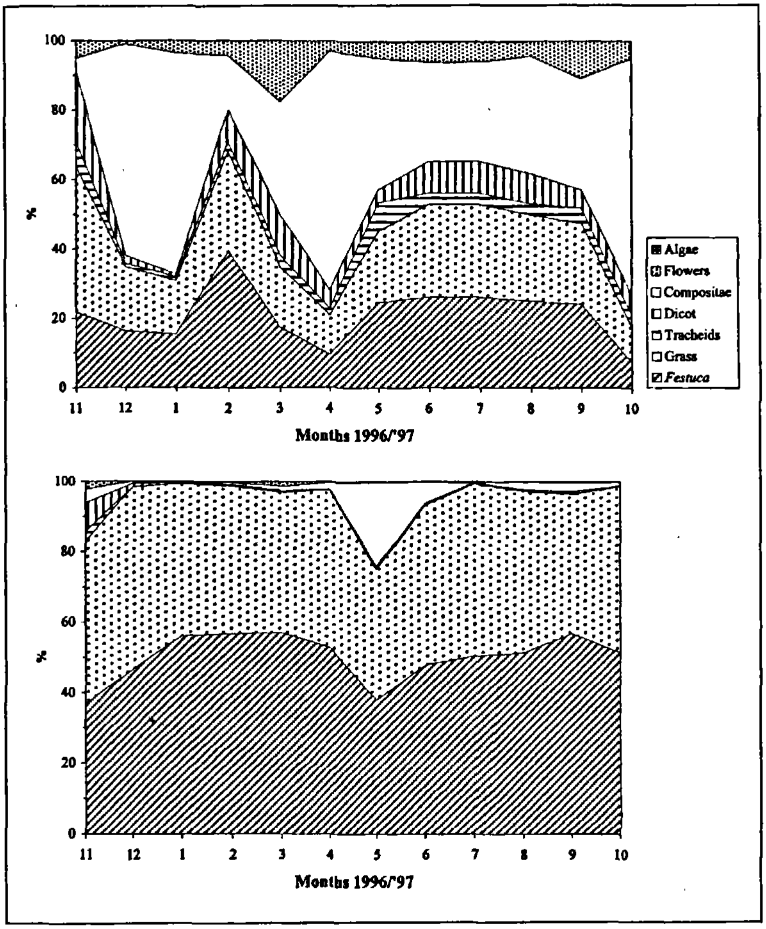
I Figure 6
Habitats of *Otomys*; *O. typus* is mainly found in the *Festuca pilgeri* grasslands shown in the foreground, *O. barbouri* in the *Helichrysum* and *Dendrosenecio* thicket in the back; Mt. Elgon, 3600 m a.s.l.



I Figure 7
Ranges (mean and variation interval) of male *Otomys barbouri* and a male *O. typus* (28. 2. - 5. 3.1999); Mt. Elgon, 3600 m a.s.l.

Festuca pilgeri grassland, while individuals of *O. barbouri* (n = 3) spent most of their time in the *Helichrysum* and *Dendrosenecio* bushes.

The maximum duration one individual could be followed up during the radio-tracking was 9 days. All radio-tracked individuals (n = 15) moved a total maximum distance of 35 m, most often to and from the same areas. Both species occurred in the same areas, but used different microhabitats (fig. 6) or have different range sizes (fig. 7).



I Figure 8
Faecal analyses, based on monthly collected pellets on Mt. Elgon, 3670 m a.s.l. for *Otomys barbouri* (top) and *O. typus* (bottom).

Although being very unsociable, which is the case in most *Otomys* species (e.g. DAVIS, 1972; DIETERLEN, 1967; VERMEUEN and NEL, 1988), the study animals did not establish territories, and their home ranges overlapped strongly, whatever the sex or species. When animals met in the field, they used to give a warning call and normally each moved away. Fights were not observed in the study. Additionally no evidence for fights, like wounded ears or tails was found.

Diet composition

The faecal analyses showed no significant fluctuation in diet composition over the year (fig. 8). The diet of *O. typus* consisted mainly of grasses of which *Festuca pilgeri* made 50%. In the pellets of *O. barbouri* all grasses together totalled about 50%, the other cell fragments were from dicotyledons, mainly parts of Compositae inflorescence.

The genus *Otomys* is a highly adapted herbivore, which relies exclusively on grass and herbs (PERRIN and CURTIS, 1980). The two species studied on Mt. Elgon were strictly herbivorous, *O. typus* feeding mainly on grasses, *O. barbouri* on grasses and dicotyledons. Food, specially grasses, is not a limiting factor for these species on Mt. Elgon. Plant phenology is not markedly seasonal (WESCHE, 2000) and flowers, a preferred food of *O. barbouri*, are supplied throughout the year.

Although one might think that the climatic conditions in the afroalpine zone have a strong influence on the rodents, *O. barbouri* and *O. typus* did not show any seasonality in the parameters studied. Reproduction, population fluctuations or weight gain or loss did not correlate with climatic variations. Both species reproduce all year round and no evidence for unfavourable seasons could be found.

Rhabdomys pumilio *(Sparrmann, 1784)*

Rhabdomys pumilio is widely distributed in South Africa and has isolated populations in montane grasslands in Tanzania and Kenya. The Mt. Elgon population is the most northern and western one. I regard this western limit of the present disjoint distribution of *R. pumilio* in East Africa as a climatic one, the mountainous areas west of Lake Victoria being probably too humid for this species.

The abundance (MNA) estimates for *R. pumilio* fluctuate in a parallel patterns on the mark-recapture grids (fig. 9). No significant difference between monthly population sizes exist between the two plots (Friedman test: $n = 9$, $\chi 2 = 2.78$, $p = 0.1$). On both mark-recapture grids the populations experienced a total population breakdown, which started with the rainy season in April 1997. The populations did not recover and the plots were not recolonized during the study period.

The population size estimates of *Rhabdomys pumilio* are negatively correlated with rainfall. The most often described pattern of popula-

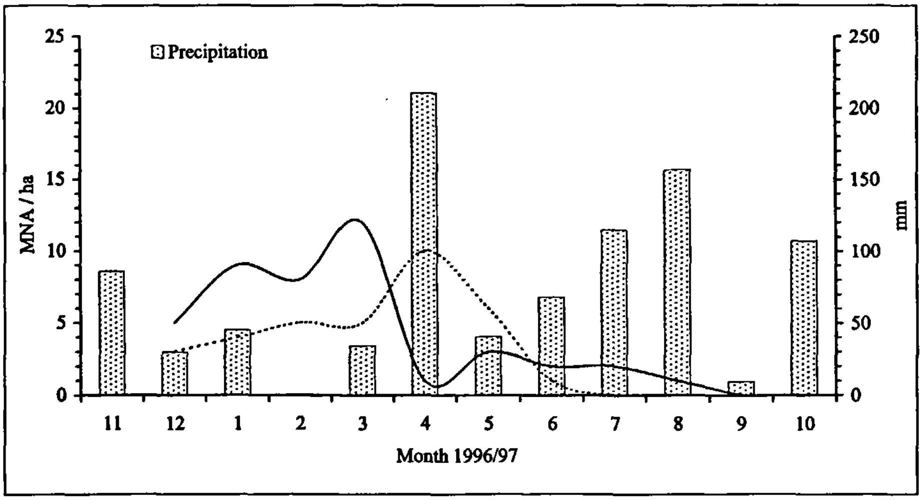


Figure 9
Population size estimates (Minimum Number Alive) for *Rhabdomys pumilio* on the two mark-recapture grids BG and GG in about 3700 m a.s.l. on Mt. Elgon from November 1996 to October 1997. The columns give the monthly precipitation measured near the grids.

tion fluctuation in African rodents is an increase in the rainy season and a decrease in the dry season (e.g. NANDWA, 1973; OGUGE, 1995). Such a pattern is generally correlated with the availability of higher nutritious food in the rainy season (e.g. FIELD, 1975; LEIRS, 1995; TAYLOR and GREEN, 1976). This relationship has been observed for *R. pumilio* as well (e.g. PERRIN, 1980) and TAYLOR and GREEN (1976) even found an increased reproduction activity when nutritive food was added experimentally.

The population fluctuations observed for *R. pumilio* on Mt. Elgon are exactly at the opposite to all other studies. There is an increase in the population size in the dry season (fig. 9), during which breeding occurs, then the population goes down again with the start of the rainy season. Food seems not to be a major trigger for *R. pumilio* reproduction on Mt. Elgon. The amount of invertebrates is significantly positively correlated with the rainfall, thus one would expect breeding and increase in population size in the rainy season. All the results for *R. pumilio* on Mt. Elgon point to a strong climatic influence on the population dynamics of this species, which is in fact highly affected by cold and humid weather conditions. For instance, the animals died very fast once they got wet (CLAUSNITZER, 2000). *Rhabdomys pumilio* probably undergoes very strong population fluctuations on Mt Elgon, with increase in dry years and strong decrease in wet years, as on the mark-recapture grids in 1997. In other areas *R. pumilio* occurred throughout the study period, its most preferred habitat being areas with open soil. Such places probably develop a good microclimate, less humid and heating up faster than places with very dense vegetation.

Fire as an important factor in landscape formation

The different grassland formations in the afro-alpine zone of Mt. Elgon, which I have discussed as important habitats for *Otomys barbouri*, *O. typus* and *R. pumilio* are the result of a long fire history. The importance of fires in afro-alpine ecosystems is well known and was described in detail by HEDBERG (1964). Mt. Elgon is mentioned as a particularly human-affected highland (HEDBERG, 1951; BECK *et al.*, 1987). The impact of fire on the ericaceous and grassland communities on Mt. Elgon was directly observed (WESCHE *et al.* in press). Fires, which are all man-made, appear to be the major agent in replacing the natural ericaceous vegetation by the grassland communities. Without fires the upper ericaceous belt up to about 4000 m a.s.l. on Mt. Elgon would naturally consist of dwarf *Erica* forest, with more open and shrubby communities only in bogs or on shallow rocky soils. Megaherbivores probably had a large impact on the vegetation, leaving open areas of different successions and size. Today relics of unburned ericaceous vegetation mainly survive in fire-safe rocky sites.

Both *Otomys* species and *Rhabdomys pumilio* benefit from the fire-induced changes from ericaceous forest towards dominating grasslands. *Otomys barbouri* prefers vegetation mosaics such as those created by rare fires. With increasing fire frequency the vegetation is converted into pure tussock grasslands, which are avoided by

O. barbouri, but inhabited in high densities by *O. typus* and *R. pumilio*. A high fire frequency results in patchy grasslands with open soil, providing optimal conditions for *R. pumilio*. This species is sensible to humid conditions in dense grasslands and seeks more open vegetation with a better microclimate. Without any fire, all three species would be very limited in their distribution, with scattered occurrences in naturally open or patchy vegetation in a dense ericaceous forest.

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