PREFACE

The present issue of the Belgian Journal of Zoology contains the proceedings of the 9th International African Small Mammal Symposium (ASMS), held at the Sokoine University of Agriculture, Morogoro, Tanzania from 14-18 July 2003

The African Small Mammal Symposia are organised every fourth year and this meeting was the first to be held in tropical Africa. There were 114 participants from 31 countries and more than half of the attending scientists were from Africa. This, as well as the many contributions from Africa in this proceedings issue, are clear indications of the growth of the community of African small mammal scientists. The large attendance to the meeting, and the publication of these proceedings, was made possible by the much appreciated financial support from the Flemish Interuniversity Council (VLIR-UOS) and the European Commission (STAPLERAT-ASMS ICA4-CT-2002-50029). Together, they contributed to travel and participation fees for 49 scientists and students from Africa and Europe.

The meeting came towards the end of the EC-supported project "STAPLERAT", on the biology and management of rodent problems in staple crops in Africa. Earlier in 2003, another project "RATZOOMAN", also funded by the EC had begun to study the role of rodents as carriers of pathogens in and around growing cities in Africa. Both projects demonstrate the heavy burden placed by rodents on the food security and health of human communities in Africa. An ecologically-based approach to management, which is highly desirable, requires a thorough knowledge of the animals basic biology and ecology. Moreover, though some species in some parts of their range are considered pests, many rodents and other small mammals are valuable parts of biodiversity. The range of topics and species covered by the contributions to this issue illustrates the variety of research that is carried out.

The publication of these proceedings was a lengthy project, stalled now and then by slow communication with authors in places where access to the internet still is not that common, changing people that assisted in keeping track of all papers and the usual burden of other commitments. We appreciated very much the assistance of N.WOUTERS, V.SLUYDTS and A.VLAEMINCK in the process. We apologise for the long delays, we thank all the authors for their patience and hope that the result is satisfying.

During the final preparations of these proceedings, we lost one of the great people in African small mammal biology. Em. Prof. dr. Walter N. VERHEYEN, from the University of Antwerp, Belgium died in December 2005 at the age of 73 years. He was a well known specialist of African rodent taxonomy and through several projects the driving force behind rodent research projects, in Tanzania and elsewhere. He was also one of the co-organisers of the first African small mammal meeting. Although he had been retired for 7 years, he continued to be active at the laboratory every day, writing papers, guiding students and colleagues and collaborating with foreign visitors who came to benefit from his knowledge. He was a mentor and friend to many of us. We dedicate these proceedings to his memory.

Herwig LEIRS, Rhodes H. MAKUNDI & Stephen DAVIS

GUEST EDITORS

We appreciated the help of the reviewers listed below that assessed and improved the papers in these proceedings and often spent considerable time correcting manuscripts and interacting with authors that were not yet so experienced in publishing scientific papers in English.

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Comparative and functional morphology of the middle ear in Zambezian mole-rats (*Coetomys – Cryptomys*, Bathyergidae)

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ABSTRACT. Within the family Bathyergidae, the genus *Coetomys* (*Cryptomys*) is the most speciose. However, an unambiguous morphological or morphometrical species diagnosis has not been feasible to date. The middle ear structures involved in sound transmission were examined and measured in six species of Zambezian mole-rats of varying body sizes : *Coetomys amatus, C. anselli, C. darlingi, C. kafuensis, C. mechowi* and *C. whytei*. Comparisons revealed many differences in the shape of the middle ear ossicles allowing species differentiation. Bullar volume, eardrum area and cross-sectional area of the bony meatus were positively correlated with body size (as represented by condylo-basal length) whereas the size of middle ear ossicles was rather independent of body size. Middle ears shared typical features with those found in low-frequency hearing mammals. Contrary to the findings in heteromyids and the *Spalax ehrenbergi* species complex, within the genus *Coetomys*, those species occupying more mesic habitats had more efficient tympano-ossicular systems (suggesting more sensitive hearing) than species from drier habitats.

KEY WORDS : middle ear, functional morphology, *Coetomys*, *Cryptomys*, species diagnosis.

INTRODUCTION

Among the five genera of the Bathyergidae (African mole-rats), representatives of the genus *Coetomys* (*Cryptomys*) can be easily recognized, yet to date it is not possible to determine different species within the genus by classical morpho-taxonomic traits like skull, pelage or size. The genus *Coetomys* is the most speciose among the bathyergid genera. At least 16 species distributed from West through Central to South Africa have been described in literature (cf., INGRAM et al., 2004). Most of the species to date have been identified within the Zambezian phytochorion. All the species have been identified on the basis of karyological, allozyme, or DNA analyses.

The existence of cryptic – yet morphologically practically indistinguishable – sibling species parallels the findings in some other subterranean rodents like blind mole-rats (*Spalax*) (NEVO et al., 2001). Nevertheless, various structures and parameters of the ear in the *Spalax ehrenbergi* species complex have proved to be of use for morphological species diagnosis (BURDA et al., 1990) supporting thus also the experience of palaeontologists and taxonomists as reflected by LAVOCAT & PARENT (1985) who noted that the auditory region serves as an excellent guide for following the evolution of the dentition. Moreover, it has been shown that in the blind mole-rat in particular (like in other subterranean mammals in general), middle ear morphology reflects also the species' habitat and way of life (BURDA et al., 1989, 1990, 1992). VON BEKESY (1974) stated that the physical laws served as guidelines for the evolution of the structures and functions of the middle and inner ear. Additionally, morpho-functional aspects of the middle ear are considered to reflect adaptations to the species' environment (e. g. WEBSTER & WEBSTER, 1975). The study of the ear has a great potential for both comparative taxonomic and functional interpretations.

Taking these facts into account we decided to study the middle ear structures in *Coetomys* species and to test their diagnostic value. Furthermore, since the selected Zambezian species also represent forms occupying different climatic regions, they provide unique opportunity to test general applicability of conclusions derived from the study of the ear in blind mole-rats (see above).

MATERIAL AND METHODS

Middle ears of six species of African mole-rats of varying body sizes (between 60 g in *Coetomys amatus* and 300 g in *C. mechowi*) representing different clades of *Coetomys* were examined. (*Coetomys* represents a newly described genus, INGRAM et al., 2004, which has been previously referred to as *Cryptomys*). They all originate from the Zambezian phytochorion : *Coetomys kafuensis* (adults N = 11, juveniles N = 1) from Itezhi-Tezhi (Zambia), *C. anselli* (adults N = 9, juveniles N = 1) from Lusaka and surroundings (Zambia), *C. amatus* (adults N = 1) from Chibale (Zambia), *C. darlingi* (adults N = 2) from Chimanimani (Zimbabwe), *C. mechowi,* (adults N = 10, juveniles N = 1) from the Copperbelt province (Zambia) and *C. whytei* (adults N = 5, juveniles N = 3) from Karonga (Malawi). All the specimens were preserved in 70%-ethanol for at least 4 weeks.

Comparative morphometry

Condylo-basal length (anterior face of the upper incisors to the posterior edge of the occipital condyles) and bullar dimensions (length of the longest axis of the bulla, width and height from the top of the auditory meatus to the bottom of the bulla tympanica) were measured with digital callipers. Middle ear structures were prepared, examined under a stereoscopic binocular and drawn using a drawing tubus at different magnifications. Measurements were taken from drawings considering the respective magnifications (15x – 40x). The following variables were measured : longer and shorter radius (perpendicular to the longest radius) of the eardrum, longer and shorter radius of the cross-section of the bony meatus, length of the mallear lever, length of the incudal lever, longer and shorter radius of the stapedial footplate. Levers were measured perpendicular to the axis of rotation from the axis of rotation to the umbo of the eardrum and to the point of action of the incus. The eardrum, meatus and stapedial footplate area were calculated as ellipses (π x longer radius x shorter radius), bullar volume was calculated as the product of length x height x width. Bullar volume, eardrum area, meatus area, mallear lever, incudal lever and stapedial footplate area were correlated with condylo-basal length (linear regression with ANOVA, SPSS 11.0).

Functional morphology

Movements of the eardrum are transmitted to the mallear-incudal complex and then to the stapes which is attached to the vestibular window of the cochlea. Through the arrangement of this ossicular chain, pressure and force are amplified. This is accomplished by two mechanisms : the difference in the area of the eardrum and the stapedial footplate leading to the area ratio and the difference in the length of mallear and incudal levers leading to the lever ratio (RELKIN, 1988). The product of both ratios (transformation ratio) expresses the middle ear efficiency in sound transmission and thus middle ear sensitivity (FLEISCHER, 1978).

Climatic data

The mean annual precipitation was calculated from monthly values from about an average of 55 years recorded by the nearest climatological station according to the Global Historical Climatological Network database : <http ://www.ncdc.noaa.gov/ol/climate/research/ghcn/ghcn.html>.

RESULTS

Comparative morphology

In the studied species, manubrium mallei and crus longum of the incus were rather parallel to each another (Fig. 1). The eardrum was nearly circular, no pars flaccida was apparent. Middle ear ossicles were not fused with the tympanic bone, so the middle ears were of the “freely mobile” type. Malleus and incus were fused whereas the incudo-stapedial joint was rather loose and the malleo-incudal complex separated easily from the stapes. A gonial was missing, the footplate area was quite large and the middle ear (stapedial and tensor tympani) muscles were reduced or missing. The anterior and posterior crura of the stapes were asymmetric, no stapedial artery was found.

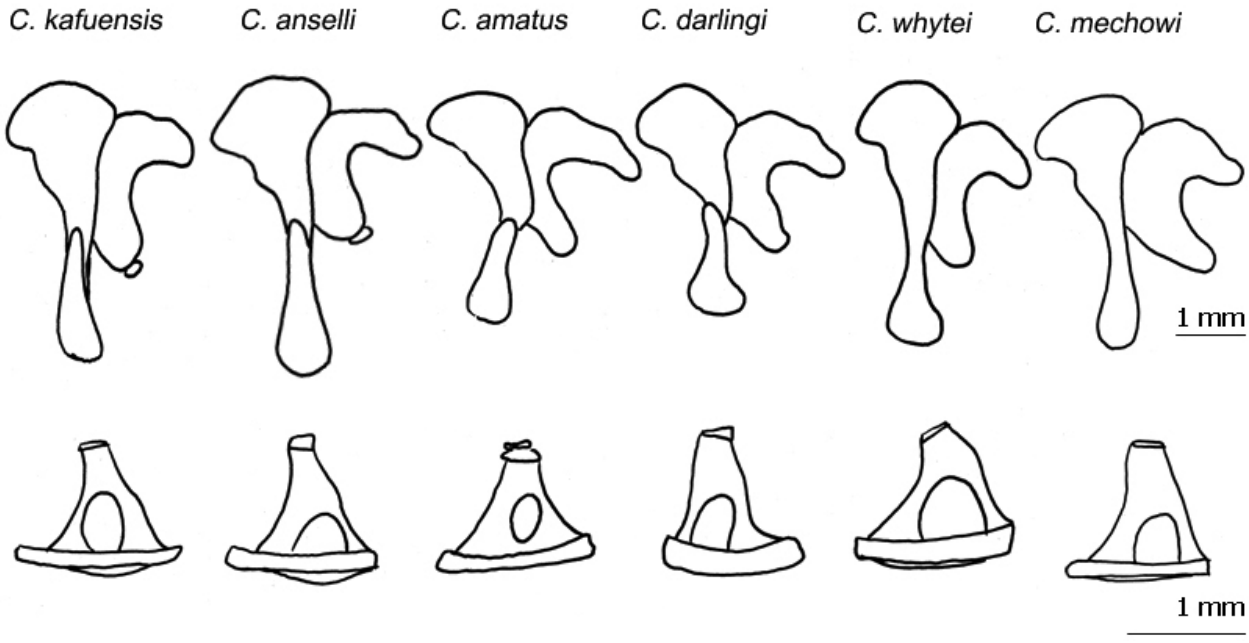

Fig. 1. – Shape of the middle ear ossicles (left - anterior, right – posterior).

The shape of the middle ear ossicles (Fig. 1) was rather similar; nevertheless some species-specific differences were identified. Thus, the head of the malleus was particularly massive in *C. whytei*. The transitional part between manubrium and head of the malleus where the tensor tympani muscle attaches was rather straight in *C. whytei* and *C. amatus*. In the other species, there was a processus which was more (*C. anselli)* or less (*C kafuensis.*) conspicuous. In *C. kafuensis* and *C. darlingi*, crus stapedis posterior was broader than crus stapedis anterior whereas the opposite was true in *C. anselli*, *C. whytei, C. amatus* and *C. mechowi*. The attachment of the stapedial muscle was clearly differently located and shaped in the studied species. Within particular species, no differences were found in shape of middle ear ossicles between adult and juvenile specimens.

Comparative morphometry

The mean values of particular parameters (Table 1) do not include juveniles. Bullar volume, eardrum and meatus area tended to be correlated with condylo-basal length. The stapedial footplate area was absolutely and relatively noticeably small in *C. amatus, C. darlingi* and *C. whytei.* Mallear and incudal lever seemed to be independent of body size.

TABLE 1

Measurements (mean values and standard deviations) of middle ear structures. in adult specimens. (LCB = condylo-basal length, Bulla = bullar volume, AM = cross-sectional area of bony meatus, MT = area of membrana tympani, BS = area of basis stapedis, ML = mallear lever, IL = incudal lever)

	N	**LCB** (mm)	**Bulla** (mm^3)	**AM** (mm^2]	**MT** (mm^2)	**BS** (mm^2)	**ML** (mm)	**IL** (mm)
C. kafuensis	11	27.8 ±1.8	321 ± 46	1.0 ± 0.2	6.8 ± 1.4	0.59 ± 0.28	2.1 ± 0.1	1.1 ± 0.2
C. anselli	9	33.1 ± 1.9	380 ± 68	0.9 ± 0.3	8.6 ± 1.1	0.53 ± 0.10	2.1 ± 0.3	1.1 ± 0.1
C. amatus	1	32.5	208	0.5	8.9	0.46	1.9	1.0
C. darlingi	2	36.2 ± 3.9	331 ± 11	0.7 ± 0.5	9.7 ± 5.8	0.48 ± 0.3	2.0 ± 0.1	1.0 ± 0.1
C. mechowi	10	45.5 ± 6.4	913 ± 302	1.4 ± 0.3	14.1 ± 2.4	0.62 ± 0.08	2.5 ± 0.2	1.3 ± 0,1
C. whytei	5	36.9 ± 1.8	469 ± 110	0.9 ± 0.1	11.6 ± 1.4	0.50 ± 0.04	2.4 ± 0.1	1.0 ± 0,1

When juvenile specimens were included into the analysis, volume of the tympanic cavity was strongly positively correlated with the condylo-basal length ($R^2 = 0.797$, $p < 0.001$, ANOVA). Eardrum area and cross-sectional area of the bony meatus were less dependent upon the body size ($R^2 = 0.299$, $p < 0.001$, ANOVA and $R^2 = 0.464$, $p < 0.001$, ANOVA) (Fig. 2). The length of mallear and incudal levers ($R^2 = 0.148$, $p = 0.01$ and $R^2 = 0.008$, $p = 0.557$, ANOVA) and the area of the stapedial footplate ($R^2 = 0.205$, $p < 0.005$, ANOVA) were rather independent of the body size (Fig. 3).

Functional morphology

The calculated functional parameters (Table 2) could be related to the mean annual precipitation in the area of occurrence of the particular species : With increasing rainfall the transformation ratio (expressing middle ear sensitivity) increased from 25 in *C. kafuensis* occurring in the driest habitat through *C. anselli* (33), *C. amatus* (37), *C. darlingi* (43), *C. mechowi* (42) to 52 in *C. whytei* living in the most mesic habitat.

TABLE 2

Precipitation in the area of occurrence and morpho-functional parameters (means and standard deviations) of the middle ear in adult *Coetomys* mole-rats of different species. (LCB = condylo-basal length AR = area ratio, LR = lever ratio, TR = transformation ratio (AR x LR))

	N	**annual precipitation** (mm/year)	**LCB** (mm)	**AR**	**LR**	**TR**
C. kafuensis	11	787	27.8 ±1.8	13.1 ± 2.2	1.3 ± 0.3	25.2 ± 6.1
C. anselli	9	822	33.1 ± 1.9	16.4 ± 4.4	2.0 ±0.4	33.2 ± 10.1
C. amatus	1	1132	32.5	19.3	1.9	36.8
C. darlingi	2	1150	36.2 ± 3.9	20.3 ± 2.7	2.1 ± 0.0	42.7 ± 5.4
C. mechowi	10	1185	45.5 ± 6.4	21.0 ± 4.6	2.0 ± 0.3	42.3 ± 14.4
C. whytei	5	1603	36.9 ± 1.8	23.2 ± 2.0	2.2 ± 0.3	52.2 ± 7.7

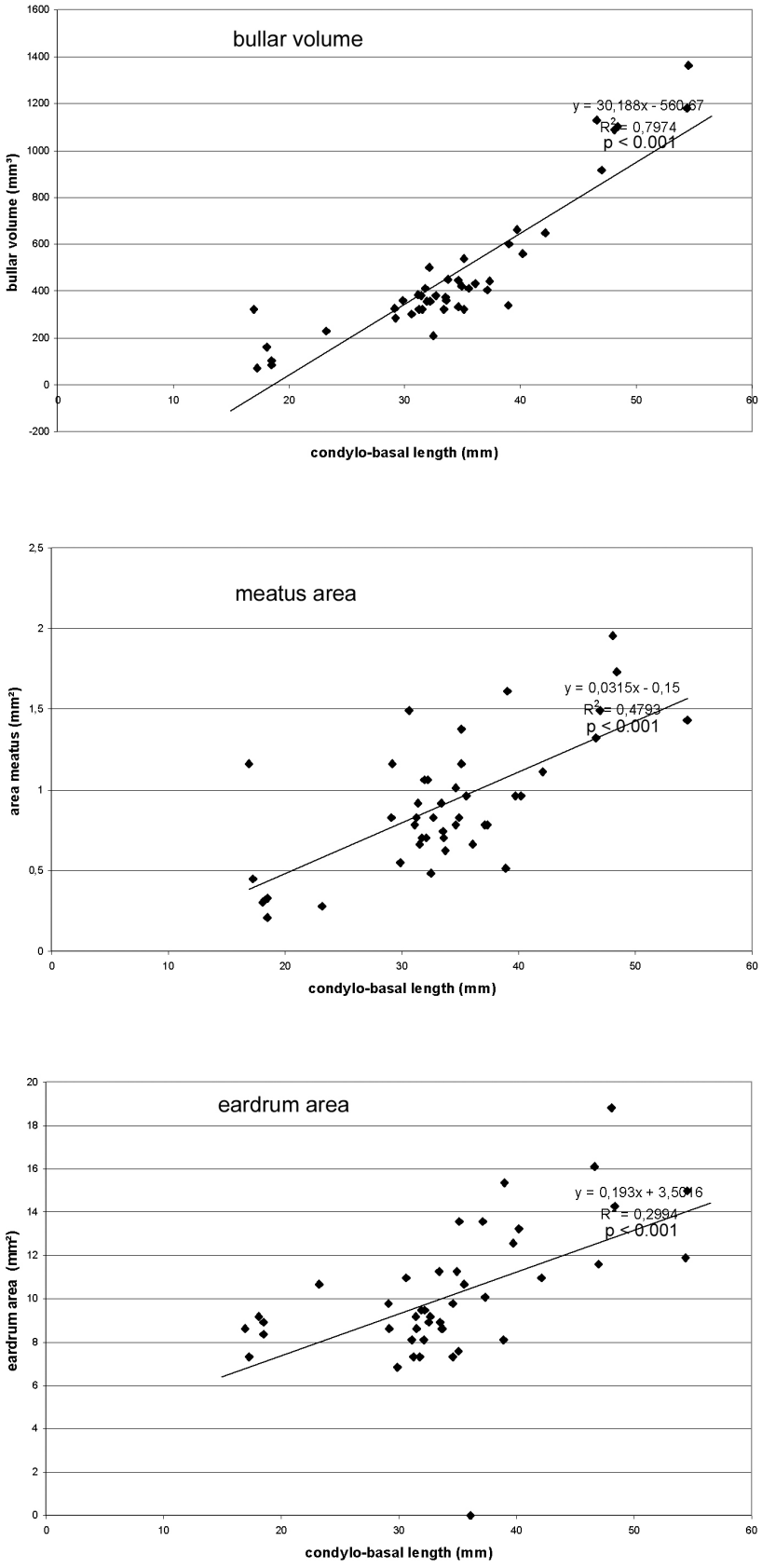

Fig. 2. – Linear regression of condylo-basal length and size of middle ear structures : bullar volume, meatus and eardrum area.

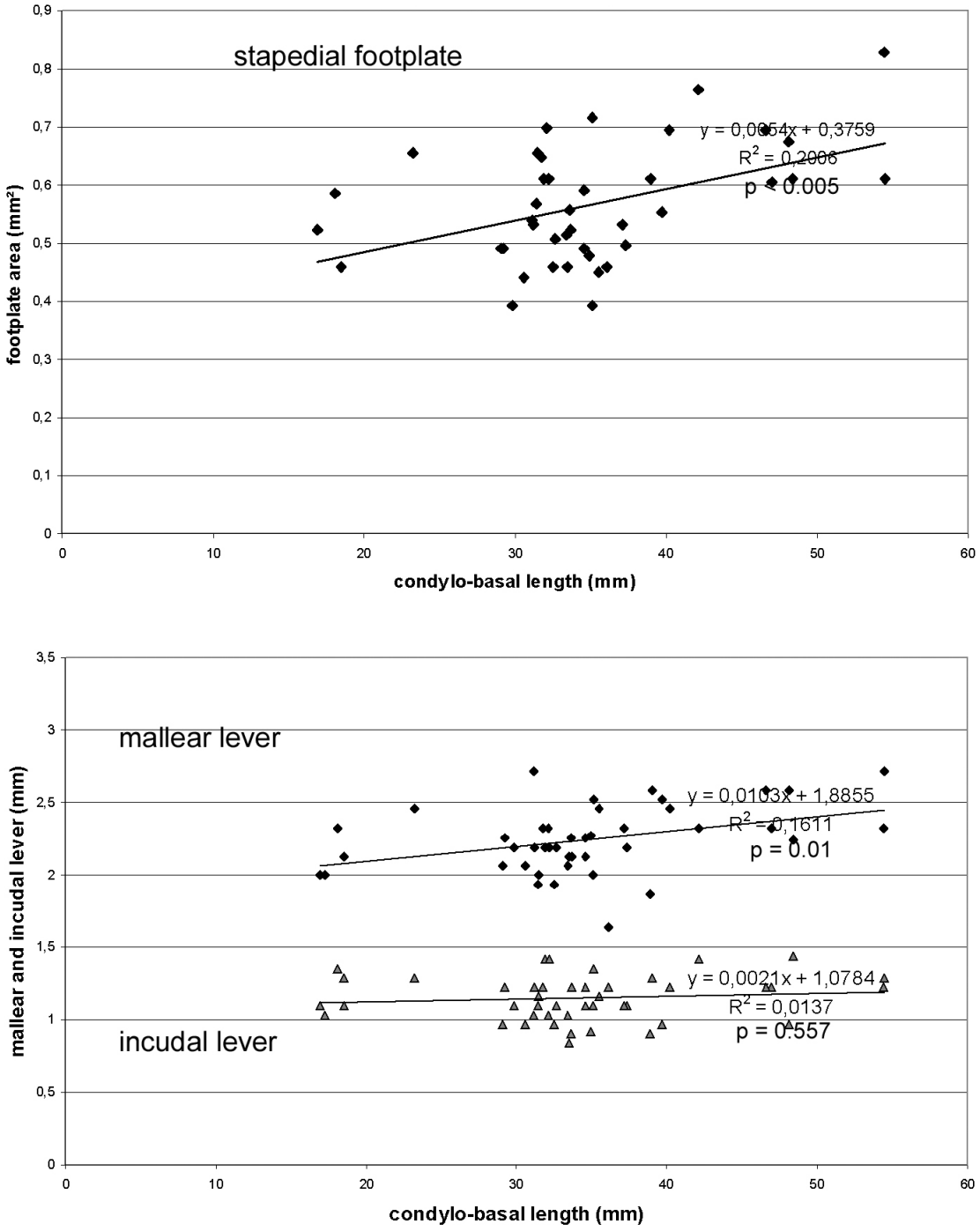

Fig. 3. – Linear regression of condylo-basal length and size of the middle ear ossicles : stapedial footplate area, mallear and incudal lever.

DISCUSSION

Comparative morphology

Morphology of the middle ear ossicles can be applied to enable species diagnosis. Although the sample sizes in *C. amatus* and *C. darlingi* are very small, there is good reason to assume that morphology described on the basis of just one or few individuals is representative of a species. Middle ear morphology is known to be a reliable species-specific trait with minimum individual variability (BURDA, 1979). Actually, in some cases it is not necessary to consider middle ear morphology if the species can be easily distinguished on the basis of the geographic origin and/or the general body size.

Since the morphology and morphometry of the middle ear ossicles (which derive from the endocranium) is almost adult-like at birth, even juvenile specimens can be reliably determined.

Freely mobile middle ears are considered as a typical trait characterizing low-frequency hearing mammals. The studied species shared with low-frequency hearing forms also other traits like fused ossicles, lacking gonial, large stapedial footplate and reduced middle ear muscles (cf., BURDA et al., 1992). These traits are considered as adaptations to optimize low-frequency hearing (MASON, 2001; FLEISCHER, 1978, 1973) in underground burrows where low frequencies of around 500 Hz are best transmitted (HETH et al., 1986) whereas lower and higher frequencies are absorbed more rapidly.

Functional morphology

In the studied species, the effectiveness of the middle ear in sound transmission increased with increasing humidity of their particular habitats. This relationship is surprising because in *Spalax ehrenbergi* (BURDA et al., 1990) and several heteromyids (WEBSTER & WEBSTER, 1980), the opposite correlation was found and interpreted as adaptation to the environment. Sound transmission is influenced by several factors from which relative humidity is one (BASS et al., 1995) : with increasing humidity attenuation first increases and after a turning point it decreases again. *Spalax* and heteromyids are adapted to the attenuation which increases with increasing aridity in their habitat. At least for heteromyids, acoustic communication over long distances and predator avoidance is of great importance (WEBSTER & WEBSTER, 1980, 1992).

REFERENCES

BASS, H.E., L.C. SUTHERLAND, A J. ZUCKERWAR, D.T. BLACKSTOCK & D.M. HESTER (1995). Atmospheric absorptions of sound : further developments. *J. Acoust. Soc. Am.*, 97 : 680-683.

BEKESY, G. V. (1974). Introduction. In : KEIDEL & NEFF (eds), *Handbook of sensory physiology. Vol. V/1, Auditory system, anatomy physiology (ear)*, Springer, Berlin : 1-8.

BURDA, H. (1979) : Morphology of the middle and inner ear in some species of shrews (Insectivora, Soricidae). *Acta Sc. Nat. Brno*, 13(4) : 1-48.

BURDA, H., V. BRUNS & G.C. HICKMAN (1992). The ear in subterranean insectivores and rodentia in comparison with ground-dwelling representatives. I. Sound conducting system of the middle ear. *J. Morph.*, 214 : 49-61.

BURDA, H., V. BRUNS & E. NEVO (1989). Middle ear and cochlear receptors in the subterranean mole-rat, *Spalax ehrenbergi*. *Hear. Res.*, 39 : 225-230.

BURDA, H., E. NEVO & V. BRUNS (1990). Adaptive differentiation of ear structures in subterranean mole-rats of the *Spalax ehrenbergi* superspecies in Israel. *Zool. Jb. Syst.*, 117 : 369-382.

FLEISCHER, G. (1973). Studien am Skelett des Gehörorgans der Säugetiere, einschließlich des Menschen. *Säugetierkundl. Mitt.,* 21 : 131-239.

FLEISCHER, G. (1978). Evolutionary principles of the mammalian middle ear. *Adv. Anat. Embryol. Cel. Biol.*, 55 : 1-70.

HETH, G., E. FRANKENBERG & E. NEVO (1986). Adaptive optimal sound for vocal communication in tunnels of a subterranean mammal (*Spalax ehrenbergi*). *Experientia*, 42 : 1287-1289.

INGRAM, C.M., H. BURDA & R.L. HONEYCUTT (2004). Molecular phylogenetics and taxonomy of the African mole-rats, genus *Cryptomys* and the new genus *Coetomys* Gray, 1864. *Molecular Phylogeny and Evolution*, 31 : 997-1014.

LAVOCAT, R. & J.P. PARENT (1985). Phylogenetic analysis of middle ear features in fossil and living rodents. *NATO ASI Series A, Life Sciences* 92 : 333-354.

MASON, M.J. (2001). Middle ear structures in fossorial mammals : a comparison with non-fossorial species. *J. Zool., Lond.*, 255 : 467-486.

NEVO, E., E. IVANITSKAYA.& A. BEILES (2001). *Adaptive radiation of blind subterranean Mole Rats*. Backhuys Publishers, Leiden.

RELKIN, E.M. (1988). Introduction to the analysis of middle ear function. In : JAHN & SANTOS-SACCHI (eds), *Physiology of the ear*, Raven Press, New York : 103-123.

WEBSTER, D.B. & M. WEBSTER (1975). Auditory system in Heteromyidae : functional morphology and evolution of the middle ear. *J. Morph.*, 146 : 343-376.

WEBSTER, D.B. & M. WEBSTER (1980). Morphological adaptations of the ear in the rodent family Heteromyidae. *Amer. Zool.*, 20 : 247-252.

WEBSTER, D.B. & M. WEBSTER (1992). Parallel evolution of low-frequency sensitivity in old world and new world desert rodents. In : WEBSTER, FAY & POPPER (eds), *Evolutionary biology of hearing*, Springer, Berlin : 633-636.

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Importance of rodents as a human food source in Benin

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ABSTRACT. Rodents are an important food source for villagers near the Lama forest reserve, located in the south of Benin between 6°55 - 7°00N and 2°04 - 2°12 E. This study was designed to look at the consumption of rodents as a food source combined with a survey of rodents sold in markets. Data was collected on : rodents species consumed, frequencies of consumption and food preferences. Some animals were captured in order to confirm the species. Rodents were a major part of diet included 10 species : grasscutter (*Thryonomys swinderianus*), giant rats (*Cricetomys gambianus*), Gambian Sun-squirrel (*Heliosciurus gambianus*), crested porcupine (*Hystrix cristata*), ground squirrel (*Xerus erythropus*), grass rat (*Arvicanthis niloticus*), slender gerbil (*Taterillus gracilis*), Kempi's gerbil (*Tatera kempii*), multimammate rats (*Mastomys spp.*) and grass mouse (*Lemniscomys striatus venustus*). On average, young people and children consumed rodents 6 times per person per month. The preferences of local populations were grasscutter and giant rats which were sold in local markets at relatively high prices US$8-10 and US$2-4 respectively. It is important to conduct further studies to look at the impact of this hunting on the rodent populations and to ensure sustainable harvesting.

KEY WORDS : Rodents, Human consumption, Lama forest, Benin.

INTRODUCTION

Little attention has been given to the beneficial effects of rodents to human food security (MENSAH, 1991; JORI et al., 1994; HANOTTE & MENSAH, 2002). In Africa, rodents are a significant source of animal protein for humans, especially in tropical Africa (AJAYI & OLAWOYE, 1974; MALEKANI & PAULUS, 1989; FALCONER, 1996; MALAISSE, 1997; NTIAMOA-BAÏDU, 1998). In Benin, there have been few studies conducted to show how important rodents are in helping to ensure the food security of the populations (BAPTIST & MENSAH, 1986; CODJIA & HEYMANS, 1988; HEYMANS & CODJIA, 1988; MENSAH, 1991; ASSOGBADJO, 2000). Therefore, a better understanding of the way rodents contribute directly to the diet of local populations is required. This study, carried out in Lama forest reserve (Bénin), describes a case study on the consumption of rodents by forest-bordering human populations.

Study site

Lama forest reserve is located in south Benin from 6°55' to 7°00' N and between 2°04' and 2°12' E (Fig. 1). It covers 16,250 ha, including 2,290 ha of dense forest as censused in 1999. The bordering populations of this forest comprise 20 rural villages with an estimated number of 41,500 individuals (1998) belonging mainly to the Holli and Fon ethnic groups. The altitude of the forest averages 60 m. Soils are vertisols of a clay-sandy type. The water network is exclusively composed of ponds and seasonal streams. The climate is a transitional guinean type, falling between the bimodal and unimodal rainfall distribution. The annual average rainfall is 1,112 mm. The annual average temperature varies between 25°C and 29°C. Relative humidity remains very high throughout the year, even in the dry season. The vegetation of the forest is composed of about 173 plant species and belongs mainly to the soudano-guinean and guineo-congolian flora. Accordingly, the natural vegetation of the forest is characterized as dense humid semi-deciduous forest. In spite of intensive poaching, it contains a rich and fairly abundant fauna that is maintained by protection activities.

MATERIAL AND METHODS

This study comprised two phases : (1) food consumption and socio-economic investigation in the bordering villages and (2) the captures of rodents in various vegetation groups and villagers' farms. A total of 126 villagers were classified into three age classes (young, adult and old) and two genders (male or female) (Table 1). Villagers between 5 to 25 years old were considered as young, an informant aged 26 to 50 years old were considered as adults, and an informant aged above 50 years old were considered as old. A structured questionnaire was used to interview individuals or a group of informants by combining retrospective method with direct observations. For examining the relative importance of rodents in the diet, data were collected from information on the consumption of other mammals to pair them with these obtained on rodents. Data were collected on the frequency of consumption and the food preferences of each species of mammals (including rodents). Practical handbooks were used to help the informant in identifying the animal species and also to obtain some useful information on it (DE VISSER et al., 2001; KINGDON, 1997; SINSIN et al., 1997; HEYMANS, 1986). The frequencies of consumption were obtained by averaging the number of times a given species was consumed per week and per informant. Three level of consumption frequency were defined as :

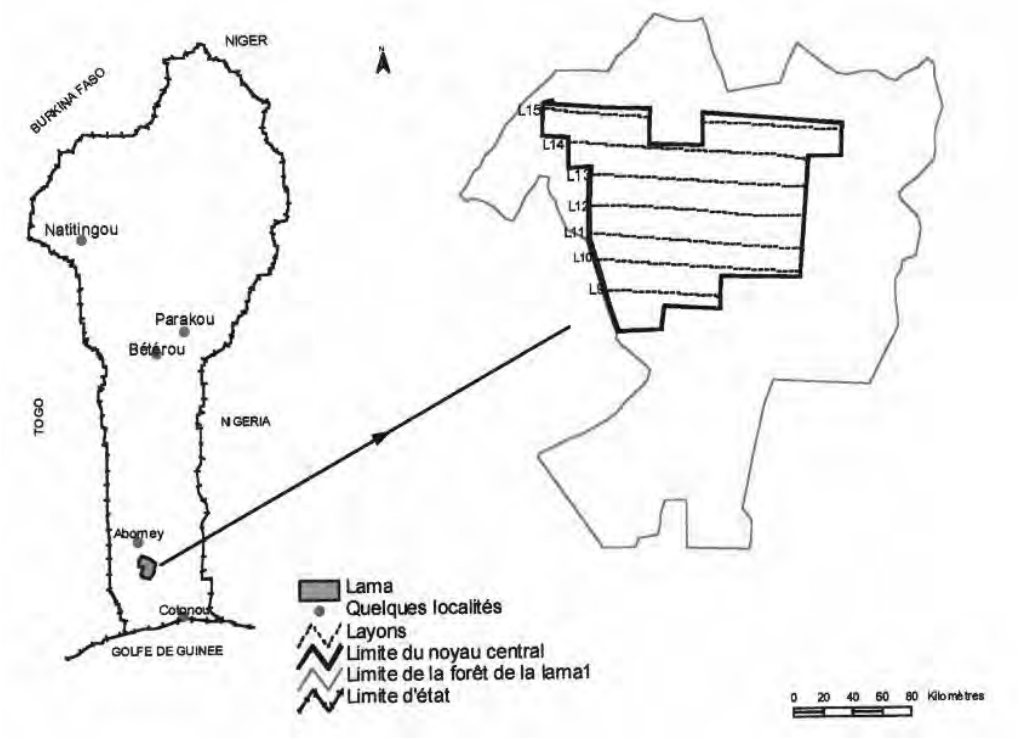

Fig. 1. – Location of Lama reserve forest in Benin

• Less consumed species : rodent species consumed by 1 to 25% of the informants

• Fairly consumed species : rodent species consumed by 26 to 50% of the informants

• Highly consumed species : rodent species consumed by more than 50% of the informants.

To capture rodents, we used a combination of several methods. We lay during 2 weeks traditional traps currently used by local population in four types of vegetation : fallow, dense and degraded forests, plantations and farms. In addition, we employed indigenous hunters to use their traditional rodent hunting techniques. Hunting takes place between 6h and 12h in the morning and between 15h and 18h in the afternoon. Regarding giant rats, villagers dug them from their burrows with a hoe before killing them and used chasing and bush fires methods for other rodents. This enabled us to survey the different traditional hunting techniques and to understand how rodents were collected from the wild.

TABLE 1

Number of local villagers (informants) who were interviewed for the study

Gender	Young	Adult	Old	Total
Male	6	25	22	53
Female	3	41	29	73
Total	9	66	51	126

NB : The age classes were defined as : young, 5-25 years old; adults, 26-50 years old; and old, >50 years old.

RESULTS

Diversity and habitats of rodents consumed by bordering populations of Lama forest reserve

Ten rodent species were consumed by local populations (Table 2) : *Thryonomys swinderianus, Cricetomys gambianus, Heliosciurus gambianus, Hystris cristata, Xerus erythropus, Arvicanthis niloticus, Taterillus gracilis, Tatera kempii, Mastomys natalensis* and *Lemniscomys striatus venustus*. These species belong to 4 rodent families namely Murideae (6 species), Sciurideae (2 species), Thryonomideae and Hystricideae (1 species for each). Although rodents were trapped in different vegetation types, villagers' farms and forests were the preferred habitats for most of rodent species consumed (Table 2)

Hunting techniques for rodents and other collecting strategies in the study area

The hunting techniques varied according to the type of animal, vegetation and season. The most common hunting techniques were chasing, trapping and using bush fires, especially at the end of the dry season before the land preparation for agriculture. Bush fires were the most frequently used technique for hunting rats.

The grasscutter (*Thryonomys swinderianus*) is the rodent species most collected by local villagers, due to the quality of its meat and the income that can be gained. Villagers hunt grasscutters in small groups of young people, by lighting bush fires to disturb the animals and flush it from the bush to be chased by dogs. Hunting takes place between 6h and 12h in the morning and between 15h and 18h in the afternoon. Giant rats (*Cricetomys gambianus*), were dug from their burrows with a hoe.

TABLE 2

Mammal species consumed by local villagers.

Scientific name	Common name	Family	Habitat type				Proportion
			For	Pla	Far	Fal	Consumed
Thryonomys swinderianus	Grasscutter	Tryonomideae	+	+	+	+	> 75%
Hystrix cristata	Crested porcupine	Hystricideae	+	+		+	> 75%
Heliosciurus gambianus	Gambian sun-squirell	Sciurideae	+	+			51-75%
Xerus erythropus	Ground squirell	Sciurideae	+	+			51-75%
Cricetomys gambianus	Giant rat	Murideae	+	+	+		> 75%
Arvicanthis niloticus	Grass rat	Murideae		+	+		> 75%
Taterillus gracilis	Slender gerbil	Murideae	+	+		+	51-75%
Tatera kempi	Kempi's gerbil	Murideae	+		+		51-75%
Mastomys natalensis	Multimammate rat	Murideae			+		51-75%
Lemniscomys striatus venustus	Grass mouse	Murideae	+		+	+	51-75%

Habitat types : For = Forest; Pla = Plantation; Far = Farm; Fal = Fallows.

Grasscutters and giant rats account for most of the cases sold after they had been captured (Table 3). Apart from these two highly preferred species, other rodent species are hunted by using bush fires, dogs and hunting. People can buy rodents in local markets for their consumption. However, this was uncommon in the study area. Hunting is still the main way for villagers to obtain rodents for animal protein. Table 3 outlines the average numbers of rodents killed per week and per hunter. This gives also the sale prices for rodent meats.

TABLE 3

Average number of rodents killed per week per hunter, and average sale prices per individual animal.

Species	Number of rodents killed	Part sold	Sale price in 1999 (US $)
Grasscutter	4	The whole	8 to 10
Giant rat	10	The whole	2 to 4
Other rodent species	15	Not sold	-

Consumption frequency for mammal and rodent species

In villages around Lama forest reserve, any kind of bush meat is considered as edible by local villagers, despite the governmental restrictions on hunting. More than 75% of the village population ate grasscutter, giant rat, grass rat and crested porcupine, while the other rodent species were consumed by 51-75% of the village population (Table 2).

Rodent meats were consumed at least 6 (Fig. 3) times per month per person. This rate was at least twice the meat consumption of other mammal species (Figs 2 & 3). The frequency of meat consumption in men is much higher than for women ($\chi^2 = 1.16$, $p < 0.05$) (Fig. 3), and the frequency of meat consumption for young people was mush higher than old people ($\chi^2 = 0.56$, $p < 0.05$) (Fig. 2).

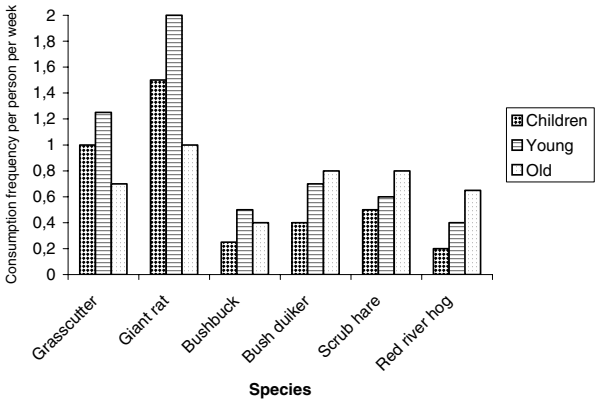

Fig. 2. – Consumption frequencies for children, young and old villagers per individual per week for the most hunted mammals in Lama reserve forest according to different age classes.

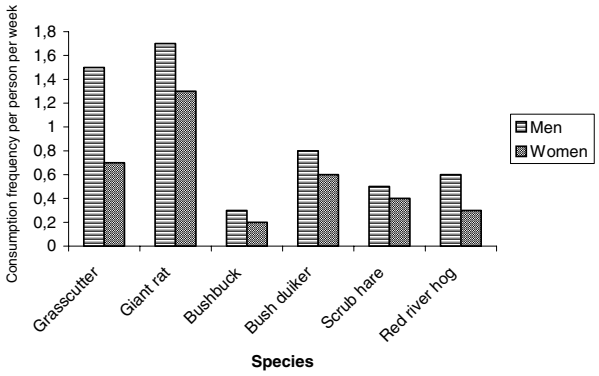

Fig. 3. – Consumption frequencies for male and female villagers per individual per week for the most hunted mammals in Lama reserve forest according to informant gender.

Local populations' consumption preference for various mammal and rodent species

More than 53% (made up of giant rat 5%, grasscutter 40%, common rat 8%) of the villagers preferred rodent meat than the meat of other mammal (Fig. 4). The red

river hog (*Potamochoerus porcus*) also was a significant source of meat (45%), with bushbuck (*Tragelaphus scriptus*) accounting for 2% of consumption.

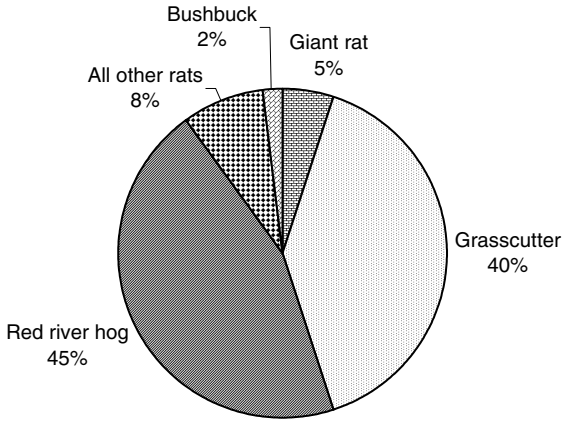

Fig. 4. – Mammals species

DISCUSSION

Wildlife constitutes an important food resource, which cannot easily be replaced or removed without causing negative socio-economic disturbances. To understand the contribution of wildlife in the food of local populations we should not consider only the big game. Most of the meat consumed by forest bordering populations in this study came from small mammals, which could be captured in any time of the year. If rodents were not available, bush meat would not be consumed by more than 60% of local populations (ASSOGBADJO, 2000). Rodents were and still are the main source of animal food for rural populations and provide an important dietary quantity of animal proteins (COLYN & DUDU, 1987; MALEKANI & PAULUS, 1989; WETCHI et al., 1988). The grasscutter and giant rat were most consumed by villagers in our study. MALAISSE (1997) showed that 100 g of grasscutter or giant rat's fresh or smoked muscle provided 28 g and 42.6 g of protein, 10 mg and 20 mg of iron, and 936 Kj and 1132 Kj energy respectively. MALAISSE (1997) also indicated that the nutritional value of rodents is similar to that of beef and chicken. In addition, these two rodent species are sold in local market at high prices, providing them with a source of income. In Lama forest reserve, the selling price for a grasscutter was US$10-12 (Table 3). In this area, a hunter killed an average of 4 individual grasscutter rats per week. This is equivalent to an income of US$40-48 per week (US$160-192 per month). This pattern is characteristic in West Africa as NTIAMOA-BAIDU (1998) reported that the incomes resulting from the sales of bush meat enable households not only to buy less expensive other source of protein such as fish, but also it helps satisfy other needs for the families. For example, in Ibadan (Nigeria), in 1975, when the meat of sheep and beef were sold respectively at US$2.80-4.20 /kg, grasscutter meat cost UD$9.60 (ASIBEY & CHILD, 1990). The hunting pressure on wildlife led to a progressive reduced availability of animal products in nearby cities where poaching was common. However, due to their high rate of reproduction, many rodent species populations were able to cope with recurrent hunting without extinction (MALAISSE, 1997). The limiting factor is much more the lack of thorough knowledge on their ecology and the density of their populations. Therefore, it would be desirable to undertake a population study in these regions to look at the impact of this hunting on the rodent populations. The hunting of wildlife, in particular rodent species as found here, provide important sources of animal proteins and incomes for local populations, and therefore should be integrated in the concept of sustainable development. The consumption of large rodents for their meat (grasscutter and giant rat) is not only a consequence of lack of meat, but also a response to a set of complex factors including cultural constraints, preferences and values. Such factors may explain why older people consumed more rodent meat than younger people in our study area and highlight the importance of these resources for rural populations of Africans.

CONCLUSION

Rodents will continue to be a considerable source of animal protein and income for villagers of Lama reserve forest. Rodents are the animal species most frequently consumed and preferred by the local populations. However, wild animals, including rodents, are not always taken into account in the national programmes for food security. Management of these resources should be included in sustainable resource initiatives that are already part of the cultural values of poor rural populations. Production in the wild and production in the extensive and intensive domestication of wild fauna can be integrated into national programmes for protected areas management. This is necessary to take into account the concerns of local populations and concurrently to satisfy requirements for keeping the balance within ecological communities.

LITERATURE CITED

AJAYI & OLAWOYE, (1974). Some indications of the social acceptance of the African rat (*Cricetomys gambianus* Waterhouse) in southern Nigeria. *Nigerian J. Forestry,* 4(1) : 36-41.

ASIBEY, E.O.A. & G.S. CHILD (1990). Aménagement de la faune pour le développement rural en Afrique subsaharienne. *Unasylva,* 161 : Vol 41.

ASSOGBADJO, A.E. (2000). Etude de la biodiversité des ressources forestières alimentaires et évaluation de leur contribution à l'alimentation des populations locales de la forêt classée de la Lama. Thèse d'ingénieur Agronome. FSA/UNB, Bénin. P. 131 + Annexes.

BAPTIST, R. & G.A. MENSAH (1986). Benin and West Africa : the cane rat-farm animal of the future? *World Animal Review,* 60 : 2-6.

COLYN, M. & A. DUDU (1987). Exploitation du petit et moyen gibier des forêts ombrophiles du Zaïre. *Nat. Fau.,* 3(4) : 22-39.

CODJIA, J.T.C. & J.C. HEYMANS (1988). Problématique liée à l'utilisation du gibier et écoéthologie de quelques rongeurs consommés au Bénin. *Nat. Fau.*, 4(4) : 4-21.

DE VISSER, J., G.A. MENSAH, J.T.C. CODJIA & A.H. BOKONON-GANTA (eds), (2001). *Guide préliminaire de reconnaissance*

des rongeurs du Bénin. C.B.D.D./Ecooperation/ReRE/VZZ - République du Bénin/Royaume des Pays-Bas. ISBN : 99919-902-1-6, 253 p.

FALCONER, J. (1996). *Sécurité alimentaire des ménages et foresterie. Analyse des aspects socio-économiques.* FAO, Rome, 1996.

HANOTTE, O. & G.A. MENSAH (2002). Biodiversity and domestication of 'non-conventional' species : a worldwide perspective. *7th World Congress on Genetics Applied to Livestock Production*, 19-23 August, 2002, Montpellier, France, 30 : 543-546.

HEYMANS, J.C. & J.T.C. CODJIA (1988). L'élevage des rongeurs : une possibilité pour résoudre le problème alimentaire en Afrique. *Rised-Bulletin*, 7 : 9-12.

HEYMANS, J.C. (1986). *Petit guide des mammifères du Nord-Bénin*. Bibliothèque FSA/UAC, Campus d'Abomey-Calavi, Bénin.

JORI, F., G.A. MENSAH & E. ADJANOHOUN (1994). Grasscutter production : an example of rational exploitation of wildlife. *Biodiversity and conservation*, 4 : 257-265.

KINGDON, J. (1997). *The kingdon field guide to African mammals*. (ed) Academic press. ISBN 0-12-408355-2. P. 465.

MALAISSE, F. (1997). *Se nourrir en forêt claire africaine : Approche écologique et nutritionnelle*. P.384. CTA.

MALEKANI, M. & J. PAULUS (1989). Quelques aspects de la consommation du cricétome, *Cricetomys* (Rongeur), par les populations zaïroises. *Tropicultura,* 4 : 60-67.

MENSAH, G.A. (1991). Élevage des espèces de gibier : cas de l'aulacodiculture. (Élevage de l'aulacode : *Thryonomys swinderianus*). Mémoire spécial. Chapitre D : Gestion du patrimoine forestier. Gestion de la faune sylvestre. *10ème Congrès Forestier Mondial "La forêt, Patrimoine de l'Avenir"*, Paris 17 au 26 septembre 1991.*Revue Forestière Française, Hors série,* 5 : 301-309.

NTIAMOA-BAIDU, Y. (1998). *La faune sauvage et la sécurité alimentaire en Afrique*. P. 109. Rome.

SINSIN, B., I. DAOUDA, E. AHOKPE, A. TEHOU, P. COUBEOU, I. TOKO & S. FANDOHAN (1997). *Faune sauvage des forêts classées de Goungoun, de la Sota et des environs*. Laboratoire d'Ecologie Appliquée FSA/UNB.

WETCHI, L., M. BIYA & J. RUELLE (1988). Observations sur l'importance relative des voies d'approvisionnement du gibier mammalien vendu au marché central de Kisangani (Zaïre). *Ann. Fac. Sci. Kis.*, 5 : 105-114.

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Pcr detection of *Leptospira* DNA in rodents and insectivores from Tanzania

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ABSTRACT. The true prevalence of leptospirosis in Tanzania is unknown or underestimated. In this study we report on the prevalence of leptospirosis in Morogoro, Tanzania, by PCR detection of leptospiral DNA in 27 kidneys of rodents (*Mastomys* spp, *Rattus* spp, and *Mus* spp) and insectivores (*Crocidura* spp). The PCR study complemented previous attempts to isolate the leptospires and to perform seroprevalence by the microscopic agglutination test (MAT). Results of this study indicated an overall detection rate of 11% by PCR, 7.4% by isolation and 0% by the MAT. Based on our analysis, it is recommended to use PCR and isolation for the detection of leptospires in potential host animals.

KEY WORDS : Leptospirosis, prevalence, microagglutination, rodents, Tanzania

INTRODUCTION

Pathogenic *Leptospira* causes leptospirosis in a wide range of mammalian hosts. Rodents are considered the primary natural reservoirs of leptospirosis in many parts of the world (ALSTON & BROOM, 1958; FAINE, 1982). In Tanzania, the true prevalence of leptospirosis is unknown or underestimated due to limited knowledge on this disease, and hence it is neglected in clinical diagnosis. The gold standard assay in leptospirosis diagnosis is the microscopic agglutination test (MAT) described by WOLF (1954). Due to the diversity of antigens within the *Leptospira* species, this method may fail to reveal infection with certain leptospiral serovars especially in a newly studied area where the prevalent (endemic) serovars are unknown, or in cases where antibody titres are low or absent. Especially in the case of animals, MAT may be specific to an infecting serovar or to antigenically closely related serovars. The chance of detecting leptospiral antibodies in a new environment, therefore, increases with the number of serovars included in the antigen panel.

Leptospires can be isolated from pathological materials (blood, cerebral spinal fluid, urine and kidney tissues), by culturing the primary specimen in selective culture media containing neomycin sulphate, sodium sulphathiozole, cyclohexamide and 5-Fluorouracil to reduce contamination (ADLER et al., 1986; ALEXANDER, 1991; FAINE, 1982). Molecular diagnosis of leptospirosis has been greatly facilitated by PCR detection of specific leptospiral DNA with specific primers that enable amplification of all saprophytic and pathogenic leptospires, as well as leptospires of ambiguous classification (MURGIA et al., 1997; MERIEN et al., 1992; GRAVEKAMP et al., 1993).

The aim of this study was to obtain molecular data for assessing the prevalence of leptospires in Morogoro, Tanzania, by PCR detection of leptospiral DNA from kidney tissues of rodents and insectivores captured in this town. This is the first report on the molecular prevalence of leptospires in an urban/periurban setting in Tanzania.

MATERIAL AND METHODS

DNA extraction from kidney tissues and PCR :

Kidneys of 20 rodents : *Mastomys* spp (18), *Rattus* spp (1) and *Mus* spp (1), and seven insectivores or shrews (*Crocidura* spp) were used. The kidney was ground in a sterile mortar containing 500 µl sterile distilled, de-ionized water. The kidney homogenate (200 µl) was used to extract DNA using the Anansa® Fast 'n' Easy Genomic DNA Purification kit (Tebu-Bio Laboratories, Cedex, France).

The PCR was carried out using specifically designed primers for the detection of pathogenic and saprophytic leptospiral DNA as described by MURGIA et al., (1997) with slight modifications. Briefly, the PCR consisted Lepat 1 (5'-GAG-TCT-GGG-ATA-ACT-TT-3') and Lepat 2 (5'-TCA-CAT-CG(CT)-TGC-TTA-TTT-T-3') primer pair for pathogenic *Leptospira*; and Sapro 1 (5'-AGA-AAT-TTG-TGC-TAA-TAC-CGA-ATG-T-3') and Sapro 2 (5'-GGC-GTC-GCT-GCT-TCA-GGC-TTT-CG-3') primers for saprophytic *Leptospira*.

DNA of known pathogenic *Leptospira* species (serovar Kenya, serogroup Ballum), and saprophytic species (serovar Patoc, serogroup Semaranga) was used as the control.

The reactions mix consisted 10 mM Tris-HCl, pH 8.3, 50 mM KCl, 200 mM of each deoxynucleoside triphosphates (dNTP), 0.5 µM of each primer, 5 µl template DNA with modified MgCl concentration (2 mM) and DNA polymerase (1 U). The PCR condition for pathogenic *Leptospira* were : initial denaturation at 93°C for 3

min then 35 cycles of denaturation at 93ºC for 1 min, primer annealing at 48ºC for 1 min, DNA extension at 72ºC for 1 min, and further 10 min extension after the last cycle. Saprophytic PCR condition were : heat denaturation at 93ºC for 3 min, then 35 cycles of heat denaturation at 93ºC for 1 min, primer annealing at 63ºC for 1.5 min, DNA extension at 72ºC for 2 min and after the last cycle extension continued for further 10 min.

Leptospira isolation from kidney tissues :

Tissue samples were prepared by grinding the freshly obtained kidneys of *Mastomys* spp (18), *Rattus* spp (1), *Mus* spp (1) and *Crocidura* spp (7) in sterile phosphate buffered saline (pH 7.2). About 0.5 ml of the kidney homogenate was inoculated in Fletcher's *Leptospira* medium containing as selective growth inhibitor, 5-Fluorouracil (200 µg/ml). The cultures were incubated at ambient temperature (26-30ºC) and examined for leptospiral growth at seven-day intervals by dark field microscopy (FAINE, 1982, 1988).

Seroprevalence of leptospires in rodents and insectivores :

The microscopic agglutination test (MAT) was used to detect leptospiral antibodies in the sera of the same rodents and insectivores used in the PCR and isolation studies. The MAT was carried out as described by COLE et al., (1973) using live antigen of five *Leptospira* serovars. The serovars were; a previously identified/proposed serovar Sokoine (MGODE et al., in Press) (serogroup Icterohaemorrhagiae); serovar Hebdomadis (serogroup Hebdomadis); serovar Hardjo (serogroup Sejroe); serovar Kenya (serogroup Ballum) and serovar Pomona (serogroup Pomona).

RESULTS

PCR of kidney tissues :

Out of 20 rodents and seven insectivores tested, three were PCR positive, generating a 330 base pair product with the Lepat 1 and Lepat 2 primers (Fig. 1). The PCR positive samples were from *Crocidura* spp., 2 of 7 (29%) and *Mastomys* spp., 1 of 18 (6%). None of the samples were PCR positive with the Sapro1 and Sapro2 primers. This finding was consistent with the presence of pathogenic leptospires.

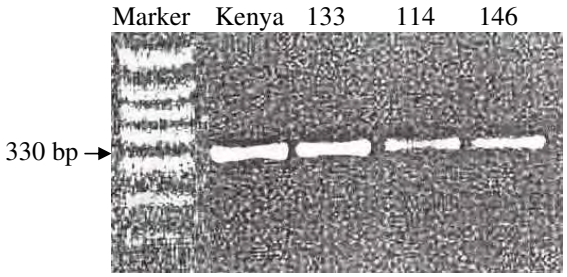

Fig. 1. – PCR products of DNA from kidneys of *Crocidura* spp (133 and 114) and *Mastomys* spp (146) with Lepat1 and Lepat2 primers. Serovar Kenya is the control pathogen, and M is the DNA ladder.
The products were separated by electrophoresis in 3% agarose and stained with ethidium bromide.

Isolation of live leptospires from kidney homogenates :

Kidney cultures of the 27 animals yielded two *Leptospira* isolates from *Crocidura* spp., derived from the same two animals that were scored positively with the PCR method.

Seroprevalence of leptospiral antibodies in rodents :

No agglutination was found in the MAT of the 27 sera against the five-leptospiral serovars used. Table 1 summarises all of these results.

TABLE 1

Comparison of leptospires detection rates by PCR, isolation and microagglutination test (MAT) in rodents and insectivores.

Test	Sample tested	Positive sample	Percent positive
PCR	27	3	11%
Isolation	27	2	7.4%
MAT	27	0	0%

Rodents (n=20) and insectivores (n=7)

DISCUSSION

The results of this study indicated a detection rate of leptospires of 11% (3/27) by PCR on the investigated cases, compared to 7.4% (2/27) by isolation and 0% by serology (MAT). The rate of *Leptospira* detection by PCR per animal species was 6% for *Mastomys* spp. and 29% for *Crocidura* spp. These relatively high infection rates could represent a hazard to public health. As there was only one individual of *Rattus* spp. and *Mus* spp. analysed with the different detection methods, it is not possible to comment on the potential infection rates of these two species. Our data suggest that leptospire detection will be highest using PCR and isolation in a situation where serological antibody detection (MAT) fails, particularly in a new study area.

Serological survey using MAT requires use of known or closely antigenically related prevalent leptospiral serovars. The use of multiple antigens from different serovars in MAT makes this test time consuming. In our study, the negative MAT results found may be due to the limited number of serovars (5) employed as antigen. This also suggests that the leptospires detected by PCR (n=3) and isolation (n=2) might posses a variant antigenic pattern, which is unrelated to that of the new putative serovar Sokoine, serovar Hebdomadis, serovar Hardjo, serovar Pomona and serovar Kenya used in the MAT. However, this is somewhat unexpected as both serovars Machang'u (isolate RM1) and Kenya (isolates Sh9 and Sh25) were recently isolated from cattle and *Cricetomys gambianus* rats in periurban Morogoro, respectively (MACHANG'U et al., 2003). These serovars were thus anticipated to be generally prevalent among rats in urban/periurban Morogoro. An alternative and more likely explanation is that the *Crocidura* spp. and *Mastomys* spp. are natural hosts for one or more of the serovars included in the MAT panel displaying low antibody titres below the detection thresh-

old of the MAT. Lower leptospiral antibody (usually IgG) levels encountered in natural hosts may indeed give MAT negative results, especially in the case of heterologous serovars (BLACKMORE et al., 1984; EVERARD & BENNETT, 1990; PALIT et al., 1991).

The success in isolation of leptospires was supported by the PCR analysis. The percentage of successful isolations may, however, not reflect the true percentage of carriership because a number of cultures (5) were lost due to contamination. Indeed contamination with less fastidious and faster growing microorganisms forms a major limitation of *Leptospira* isolation in spite of the fact that contamination can be kept at minimum by deploying selective growth inhibitors such as 5-Fluorouracil in the culture medium.

As MAT can fail to reveal leptospires carriership in some host animals, it is recommended that PCR and isolation methods are also used, where feasible, to investigate infection sources. These methods are particularly important when carrying out studies in area with unknown leptospirosis prevalence. Rodents and insectivores should be considered important reservoirs of leptospires in the Morogoro area and can serve as indicators of leptospirosis prevalence.

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REFERENCES

ADLER, B., S. FAINE, W.L. CHRISTOPHER & R.J. CHAPPEL (1986). Development of an improved selective medium for isolation of leptospires from clinical material. *Veterinary Microbiology*, 12 : 377-381.

ALEXANDER, A.D. (1991). *Leptospira*. In : BALOWS, A., W.J. HAUSLER, K.L. HERMANN, H.D. ISENBERG & H.J. SHADONY (eds), *Manual of clinical microbiology 5th ed.* American society for microbiology, Washington.

ALSTON, J.M. & J.C. BROOM (1958). *Leptospirosis in man and animal.* E & S. Livingstone, Edinberg and London.

BLACKMORE, D.K., L.M. SCHOLLUM & K.M. MORIARTY (1984). The magnitude and duration of titres of leptospiral agglutinins in human sera. *New Zealand medical journal*, 97 : 83-86.

COLE, J.R., C.R. SULZER & A.R. PURSELL (1973). Improved microtechnique for the leptospiral agglutination test. *Applied Microbiology*, 25 : 976-980.

EVERARD, C.O.R. & S. BENNETT (1990). Persistence of leptospiral agglutinins in Trinidadian survey subjects. *European journal of epidemiology,* 6 : 40-44.

FAINE, S. (1982). *Guidelines for the control of leptospirosis*. World Health Organization, Geneva.

FAINE, S. (1988). *Leptospirosis*. In : BALOWS A, W.J. HAUSLER, E.H. LENNETTE, M. OHASHI & A. TURANO (eds), *Laboratory diagnosis of infectious diseases. Principles and practice. Vol. 1. Bacterial, mycotic and parasitic diseases.* Springer-Verlag, New York.

GRAVEKAMP, C., H. VAN DE KEMP, M. FRANZEN, D. CARRINGTON, G.J. SCHOONE, G.J.J.M. VAN EYS, C.O.R. EVERARD, R.A. HARTSKEERL & W.J. TERPSTRA (1993). Detection of seven species of pathogenic leptospires by PCR using two sets of primers. *J. Gen. Microbiol.,* 139 : 1691-1700.

MACHANG'U, R., G. MGODE, J. ASENGA, G. MHAMPHI, R. HARTSKEERL, M. GORIS, C. COX, B. WEETJENS & R. VERHAGEN (2003). Characterisation of *Leptospira* isolates from captive giant pouched rats, *Cricetomys gambianus*. In : SINGLETON, G.R., L.A. HINDS, C.J. KREBS & M.D. SPRATT (eds), *Rats, Mice and People, Rodent Biology and Management.* Australian Centre for International Agricultural Research, Canberra 2003.

MERIEN, F., P. AMOURIAUX, P. PEROLAT, G. BARANTON & I. SAINT GIRONS (1992). Polymerase chain reactions for detection of *Leptospira* species in clinical samples. *Journal of clinical microbiology,* 30 : 2219-2224.

MGODE, G.F., R.S. MACHANG'U, M.G. GORIS, M. ENGELBERT, S. SONDY § R.A. HARTSKEERL (in press). New *Leptospira* serovar Sokoine of serogroup Icterohaemorrhagiae from cattle in Tanzania. *Int. J. Syst. Epidemial Microbiol.*

MURGIA, R., N. RIQUELME, G. BARANTON & M. CINCO (1997). Oligonucleotides specific for pathogenic and saprophytic leptospira occuring in water. *FEMS Microbiol. Lett.*, 148 : 27-34.

PALIT, A., C. HOSKING, L. CREATE, J. MORTON & S. FAINE (1991). Leptospirosis in dairy farmers of Western Victoria, Australia. In : KOBAYASHI Y. (ed.), *Leptospirosis.* Proceedings of the Leptospirosis Research Conference (1990). Hokusen-Sha, Tokyo.

WOLF, J.W. (1954). *The laboratory diagnosis of leptospirosis*. Thomas publishers, USA.

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Investigating the role of natural gallery forests outside the Congolese rainforest as a refuge for African forest shrews

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ABSTRACT. Conditions that prevailed in rainforest faunal refuges during glacial periods of the Pleistocene, particularly their size, position and habitat characteristics, remain little investigated. After the peak of the last interglacial period of the Holocene (7000 years B.P.), the Guineo-Congolese rainforest has been reduced in size and isolated gallery forests emerged in the peripheral Northern Congo forest-savanna mosaic, mainly because of the reduction in rainfall. In the north of the Central African Republic, 400 km north of the present rainforest zone, up to the Sudano-Sahelian savannas, such gallery forests harbour several forest species of plants, birds and mammals related to West and/or East Congo faunal regions. This suggests that since the catastrophic destruction of central African rainforests, that culminated about 2500 years ago, these galleries could have mimicked the conditions that occurred in the Pleistocene refuges. We tested whether these natural gallery forests, outside the Congolese rainforest, could act as refuges for small forest mammals such as shrews. Composition and structure of shrew communities were studied in three main regions belonging to three river basins and two distinct phytoregions. They were compared to two other shrew communities located within the main Congolese rainforest, also in C.A.R.. None of the typical rainforest shrew species was collected within the studied isolated gallery forests. Thus, climatic and habitat characteristics within these gallery forests were presumably not suitable for these forest patches to act as climatic refuges for the forest shrew fauna.

KEY WORDS : Soricidae, *Crocidura*, *Suncus*, Central African Republic, Community structure, Biogeography, Refuge theory.

INTRODUCTION

In the Quaternary period (from 1.8 My B.P. to present), Africa underwent climatic oscillations resulting in several phases of forest fragmentation and extension. During the last glacial maximum of the Pleistocene (between about 20000 and 15000 years B.P.), as a result of the very cold and dry climate, tropical rainforest decreased in size and became fragmented. Paleontological and biogeographic data suggest that it was limited to lowland forest patches in the downstream zone of the large rivers and on lower slopes of mountains (HUTTERER et al., 1987; MALEY, 1987; COLYN, 1991; COLYN et al., 1991; MALEY, 1996; MALEY & BRENAC, 1998). According to HAFFER (1969), these forest patches may have acted as refuges for the forest flora and fauna. In contrast, during the inter-glacial periods, the warmer and wetter climate favoured an extension of the rainforest. The last inter-glacial period culminated at 7000-8000 years B.P., during the Holocene (MALEY, 2001). The central African rainforest extended to the north, up to the present Sudano-Sahelian savanna zone. Since 5000 years B.P., the reduction in rainfall (BERTAUX et al., 2000), associated with climatic disturbance, resulted in contraction of the central African rainforests that culminated about 2500 years ago (MALEY, 2001). In the north of the Central African Republic (C.A.R.), since 7000 years B.P., the extension of the savannas (MALEY & BRENAC, 1998) resulted in the isolation of gallery forests outside the Congolese rainforest. Despite a new phase of forest extension that began 2000 years ago (MALEY, 2001), it is probable that these Holocene gallery forests remained isolated from the Congolese rainforest and could have acted as forest refuges. It is hypothesised that Pleistocene and Holocene refuges probably formed a network of forest isolates within a forest-savanna mosaic zone rather than small homogenous forest isolates (LEAL, 2000; MALEY, 2001). The principal refuges of the Pleistocene were probably located in the downstream zone of the large rivers, within the present rainforest zone. However, the conditions that prevailed in

these forest refuges, particularly their size and habitat characteristics remain poorly investigated.

In the North of the C.A.R., more than 400 km north of the present northern boundary of the rainforest, Holocene gallery forests are known to harbour typical Congolese forest plants, birds and mammals (FAY, 1988; CHRISTY, 1999; ECOFAC, 2001). These taxa also occur in the West Central or East Central regions (*sensu* COLYN, 1999; COLYN & DELEPORTE, 2002b) and these galleries represent their northernmost range limit. In particular, FAY (1988) showed that three strictly arboreal species of forest primates (*Cercopithecus pogonias*, *C. nictitans* and *C. ascanius*), known to be widely distributed in the Congolese rainforest, can be found in the northern C.A.R. gallery forests, in the south-western sector of Manovo-Gounda-St. Floris National Park. The aim of this study is to test whether these natural gallery forests, located outside the Congolese rainforest, may act as refuge for terrestrial small forest mammals such as shrews. This may help to understand the conditions that could have prevailed in the Pleistocene refuges.

MATERIAL AND METHODS

Study area

The study area (80000 km^2) is located in the north of C.A.R., more than 400 km north of the present northern boundary of the Congolese rainforest (Fig. 1). It has been managed until the end of the year 2000 by the "Programme de Développement de la Région Nord" (P.D.R.N.). Since then, it has been associated with the ECOFAC project under the name "Zones Cynégétiques Villageoises" (Z.C.V.). Shrews were collected at eleven sites (Fig. 1) located within National Parks (Bamingui-Bangoran N.P., sites 5-7; Manovo-Gounda-St Floris N.P., 8-9 and its periphery, 10), within a hunting zone (Sangba, sites 3 and 4) or in neighbouring zones (sites 1, 2 and 11) within the project's action area (TÉLLO, 2000; ECOFAC ONLINE). All these sites, which are located in the upstream zone of several rivers, were pooled in three main regions : Bohou (sites 1 and 2), Bamingui-Bangoran (sites 3-7) and Manovo-Mara (sites 8-11) They belong to three river basins (Bahr Aouk, Bamingui and Kotto) and two distinct phytoregions (medio-Sudanian savanna and Sudano-Sahelian savanna; (Table 1; Fig. 1).

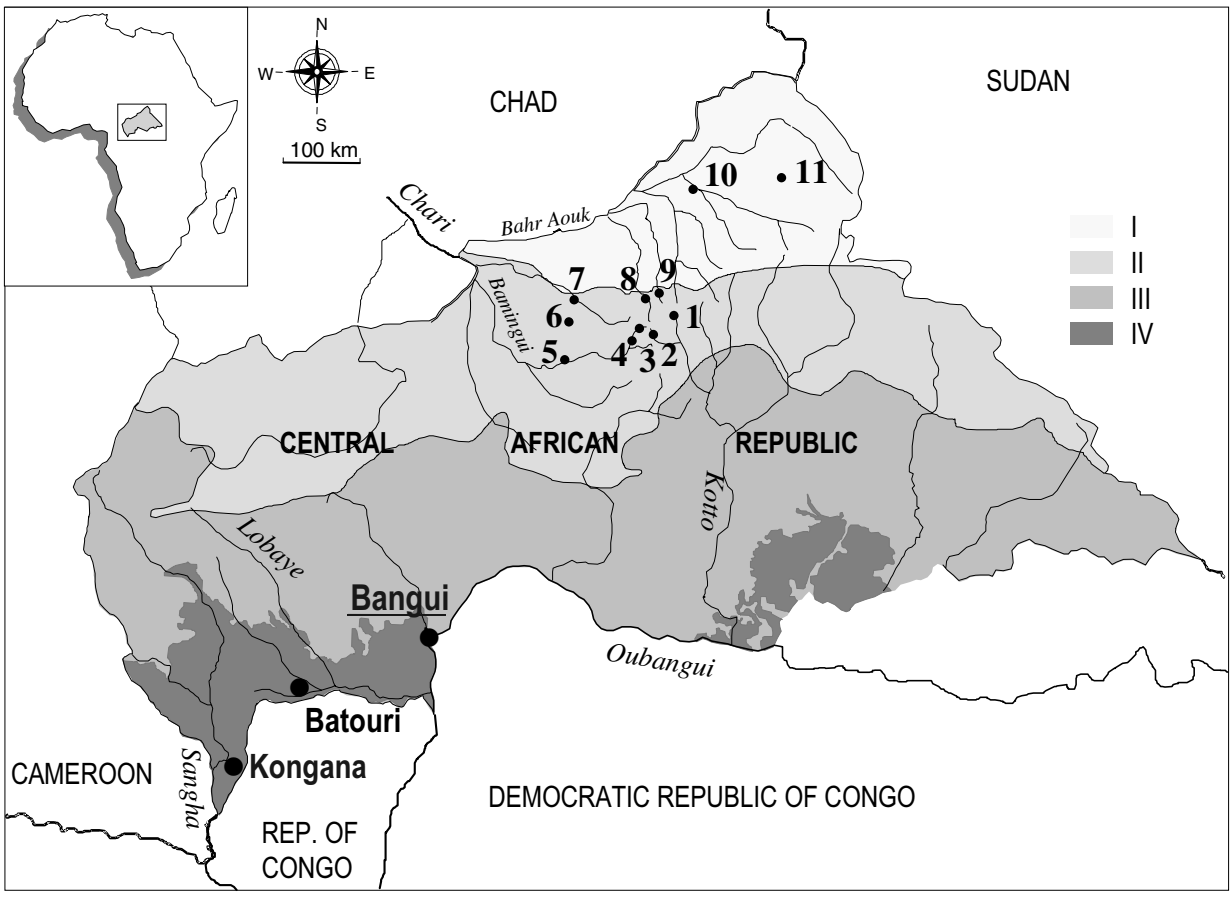

Fig. 1. – Study sites in the north of the Central African Republic : 1, Kpata; 2, Bohou; 3, Bamingui-Brendja; 4, Sangba; 5, Kaha pond, near Bamingui; 6, Kivou pond; 7, Bangoran; 8, Manovo; 9, Koumbala; 10, Gordil; 11, Délembé. Phytoregions *sensu* BOULVERT (1986) : I, Sudano-Sahelian savanna; II, medio-Sudanian savanna; III, Sudano-Guinean savanna and peri-forest sector of the Guineo-Congolian rainforest and savanna domain; IV, rainforest sector of the Guineo-Congolian domain. The two sites located within the Congolese rainforest and selected for comparison (Batouri and Kongana) are also plotted.

The Bohou region is located in the upstream zone of the Kotto River within the Congo River basin, while the two other regions are located in the upstream zone of the Chari River, within the Chad River basin. A savanna zone of ca. 5 km has been separating the two river basins for the past few hundred years (FAY, 1988). The southernmost sites (1-9) belong to the medio-Sudanian savanna domain *sensu* BOULVERT (1986), while the other two (10 and 11) belong to the Sudano-Sahelian savanna. The typical medio-Sudanian sector is of *Encephalartos septentrionalis* type at the sites 1-4 and 8-9, with included bamboo savannas of *Oxytenanthera abyssinica* type (e.g. site 3), and of *Butyrospermum paradoxum parkii* type at sites 5-7 (BOULVERT, 1986). It harbours gallery forests of *Anogeissus leiocarpus* type at all sites (1-9). The northernmost sites (10, 11) belong to the Sudano-Sahelian domain and are of *Terminalia lexiflora* type.

TABLE 1

Characteristics of each study site. Site numbers refer to Figure 1. Main habitat types : BS, bamboosian savanna; GF, gallery forest; RS, riparian savanna; S, undifferentiated savanna.

Site No	Study Site	Coordinates	Main Region	Main habitat		Sub-climate	Annual Rainfal (mm)
				GF	S		
1	Kpata	08°03'N; 21°24'E	Bohou	GF		sub-Sudanian	1200-1400
2	Bohou	07°43'N; 21°20'E	Bohou	GF		sub-Sudanian	1200-1400
3	Bamingui-Brendja	07°47'N; 20°57'E	Bamingui-Bangoran	GF	BS	sub-Sudanian	1200-1400
4	Sangba	07°45'N; 20°43'E	Bamingui-Bangoran		RS	sub-Sudanian	1200-1400
5	Kaha pond near Bamingui	07°26'N; 20°08'E	Bamingui-Bangoran	GF	S	sub-Sudanian	1000-1200
6	Kivou pond (= Kaga Yara)	07°51'N; 20°11'E	Bamingui-Bangoran		RS	sub-Sudanian	1000-1200
7	Bangoran	08°05'N; 20°21'E	Bamingui-Bangoran		S	sub-Sudanian	1000-1200
8	Manovo	08°22'N; 20°57'E	Manovo-Mara		RS	sub-Sudanian	1200-1400
9	Koumbala	08°19'N; 21°17'E	Manovo-Mara	GF		sub-Sudanian	1200-1400
10	Gordil	09°36'N; 21°41'E	Manovo-Mara		RS	Sudano-Sahelian	1200-1400
11	Délembé	09°44'N; 22°39'E	Manovo-Mara		RS	Sudano-Sahelian	1000

All the sites have a Sudano-Guinean climate, with sub-Sudanian or Sudano-Sahelian sub-climates (Table 1). Gallery forests were surveyed in each of the three regions, and the surrounding savanna was also surveyed within the Chad River basin (Table 1). Sampling in different river basins and phytoregions, rather than focusing on sampling within a single gallery forest, was considered the best way to have a good representation of the shrew community in the study area. Human populations in the area have a density lower than 0.5 persons/km^2 and have a low disturbance effect on the small mammal fauna, especially on shrews that are never hunted nor eaten.

Two sites located within the Congolese rainforest were selected for comparison (Fig. 1). The Batouri River site, in the Ngotto forest, consists of a mixed-species semi-deciduous rainforest at the northern limit of the Guineo-Congolese rainforest (more details in BOULVERT, 1986). This primary rainforest is often affected by storms and numerous tree falls have created openings in the canopy (BARRIÈRE et al., 2000). With a typical forest Guinean climate, the rainfall, occurring mainly from May to October, averages 1600 mm per year. The Kongana study area consists mainly of a mixed-species semi-deciduous rainforest and a mono-dominant *Gilbertiodendron dewevrei* forest, and has a climate similar to that of Ngotto (RAY & HUTTERER, 1996).

Sampling

Trapping was mainly performed from May to August 1998 and from June to August 1999 (Table 2), i.e. during the early wet season, by J.L. TÉLLO and/or a member of the University of Rennes 1. Our major method of collecting shrews was by dry, not-baited pitfall traps, with 10-litre buckets positioned at 5 m intervals along a linear plastic drift fence. All the lines were constructed as described in NICOLAS et al. (2003). Trapping period, number of pitfall lines and cumulated trapping effort varied between sites (Table 2). The thirty-five pitfall lines totalled a pitfall trapping effort of 8581 bucket-nights.

Mixed Sherman traps and metal snap-traps were also used in transects, mainly to capture rodents, and totalled 32844 trap-nights. In addition, a few specimens were incidentally collected by J.L. TÉLLO since June 1997. Most of the small mammals captured were weighed, measured, autopsied and preserved in 10% formalin. Species identification was performed by two of the authors (R.H. and P.B.) on the basis of morpho-anatomical analyses, and in some instances supported by molecular analyses (QUÉROUIL et al., 2001; in press). The taxonomic nomenclature follows HUTTERER (1993), except for *Suncus megalura*, previously considered as a *Sylvisorex* species, but now considered as a *Suncus* species according to QUÉROUIL et al. (2001). Three problematic *Crocidura* taxa, belonging to species complexes still in need of revision, were named *Crocidura* cf. *denti*, *C.* cf. *hildegardeae* and *C.* cf. *poensis* as they could not be definitively identified. The material was deposited at the Station Biologique de Paimpont, University of Rennes 1, France and the Museum Alexander Koenig, Bonn, Germany.

Data analysis

The trapping effort (TE, in trap-nights) was defined as the number of traps (or buckets) set for a 24-hour period, and the trap success (TS) as the number of individuals captured per 100 trap-nights; i.e. TS = (N/TE)*100, where N is the number of shrews captured. Genus and species richness (G and S) were defined as the number of distinct genera and species identified, respectively. Spe-

cies relative abundance (pi, %) was defined as the number of individuals (ni) of species i captured per 100 individuals of all species, i.e. pi = (ni/N)*100. For the estimation of species richness, all shrew captures were considered, but for the estimation of trap success and species relative abundance, only the individuals captured by pitfall traps were selected.

TABLE 2

Trapping characteristics (trapping period, number of lines and trapping effort, mainly in pitfall (P)), shrew trap success, identity and number of shrews captured. Site numbers refer to Table 1 and Figure 1. Number of shrews collected in mixed Sherman and metal snap-traps line (L) are in brackets and those collected by hand (H) in square-brackets. Main habitat type codes refer to Table 1. A species code (A-N) was attributed to each shrew taxon.

Main region	**Bohou**		**Bamingui-Bangoran**							**Manovo-Mara**				**Total**			
Site number	**1**	**2**	**3**		**4**	**5**		**6**	**7**	**8**	**9**	**10**	**11**				
Mean of collect	**P**	**L**	**P**	**P**	**P**	**P**	**H**	**P**	**L**	**L**	**P**	**P**	**P**	**P**	**L**	**H**	**Total**
Main Habitat type	**GF**	**GF**	**GF**	**BS**	**RS**	**GF**	**S**	**RS**	**S**	**RS**	**GF**	**RS**	**RS**				
Trapping period	Jun-98		May-98	Aug-98	Aug-99	Jul-99		Jul-99			Jul-98	Jun-99	Jun-99				
No of pitfall lines	4		5	3	4	4		4			6	3	2	35			
Trapping effort (TE)	1,584		1,500	648	700	900		700			1,584	600	365	8,581	32,844		
No of shrews captured (N)	58	(1)	41 (1)	26	29 [4]	23	[1]	16	(4)	(4)	47 (2)	23 [4]	7 (1)	270	(13)	[9]	292
Trap success (TS)	3.66		2.73	4.01	4.14	2.56		2.29			2.97	3.83	1.92	3.15	0.04		
A *Crocidura* cf. *denti* Dollman, 1915	4	(1)	15	4	4 [1]	5		2			18 (1)	1 [1]		53	(2)	[2]	57
B *Crocidura* cf. *hildegardeae* Thomas, 1904			23 (1)	4	16	1	[1]	6			2	1	1	54	(1)	[1]	56
C *Crocidura* cf. *poensis* (Fraser, 1843)					2					(1)		12 [1]	3 (1)	17	(2)	[1]	20
D *Crocidura fuscomurina* (Heuglin, 1865)					1									1			1
E *Crocidura lamottei* Heim de Balsac, 1968	1								(2)					1	(2)		3
F *Crocidura littoralis* Heller, 1910	4					9					5			18			18
G *Crocidura ludia* Hollister, 1916	41													41			41
H *Crocidura nanilla* Thomas, 1909								1					1	2			2
I *Crocidura olivieri* (Lesson, 1827)	5		1	4	2 [3]	1		7	(2)	(3)	3 (1)	1	1	25	(6)	[3]	34
J *Crocidura roosevelti* (Heller, 1910)	1			2							1			4			4
K *Crocidura turba* Dollman, 1910												[2]				[2]	2
L *Crocidura yankariensis* Hutterer & Jenkins, 1980												7		7			7
M *Suncus infinitesimus* (Heller, 1912)	2		2	7	2	6					18	1	1	39			39
N *Suncus megalura* (Jentink, 1888)					2									2			2
Specimens not seen				5		1								6			6
Genus richness (G)	2	1	2	2	2	2	1	1	1	1	2	2	2	2	1	1	2
Species richness (S)	7	1	4	5	7	5	1	4	2	2	6	7	5	13	5	5	14

RESULTS

Overall community composition

A total of 292 shrews representing two genera and fourteen species were collected. One genus (*Suncus*) was only represented by two species and the other one (*Crocidura*) by 12 species (Table 2). More than ninety-two percent of shrews were collected in pitfall traps (N=270; TS=3.15) while only 13 individuals were captured in Sherman traps (TS=0.04), nine were collected by hand and none in metal snap-traps. While only five species were trapped in Sherman traps, thirteen species were captured in pitfalls. *Crocidura turba* was only collected by hand. Two species were numerous (*C.* cf. *hildegardeae* and *C.* cf. *denti*, each comprising about 20% of all shrews), five were common (*C. ludia*, *S. infinitesimus*, *C. olivieri*, *C.* cf. *poensis* and *C. littoralis*) and the other seven were captured infrequently. The three specimens of the savanna species *C. lamottei*, described from Lamto (Ivory Coast) and since then widely recorded within Sudanian and Guinean savannas from Senegal to western Cameroon, constitute the first known record of the species in C.A.R. and the easternmost limit of its distribution range. The seven specimens of the uncommon savanna shrew *C. yankariensis* also constitute the first known record of the species in C.A.R.

Community structure within the gallery forests

In the gallery forests, with a pitfall trapping effort of 5568 bucket-nights, 169 shrews (TS=3.04) representing two genera and eight species were recorded (Fig. 2a). The two genera (*Crocidura* and *Suncus*) were captured in each of the three main regions. The number of species varied from five to seven according to the region. It is noteworthy that the shrew community had a higher species richness and trap success at Bohou (S=7 and TS=3.66, respectively), within the Congo River basin. All the species recorded are either savanna species or species occurring within the rainforest and at its margin (see Table 3) but preferentially in open habitat. *Crocidura ludia*, the most forest-dependent species amongst the recorded species, was highly dominant at Bohou, while it was absent from all pitfall traps in the Chad River basin. Within the latter, the structure of the community differed between the two studied regions : the medium-sized *C.* cf. *hildegardae* was more abundant at Bamingui-Bangoran (pi=37.5%) while the medium-sized *C.* cf. *denti* and the tiny *S. infinitesimus* co-dominated in the Manovo-Mara region (pi=38.3%).

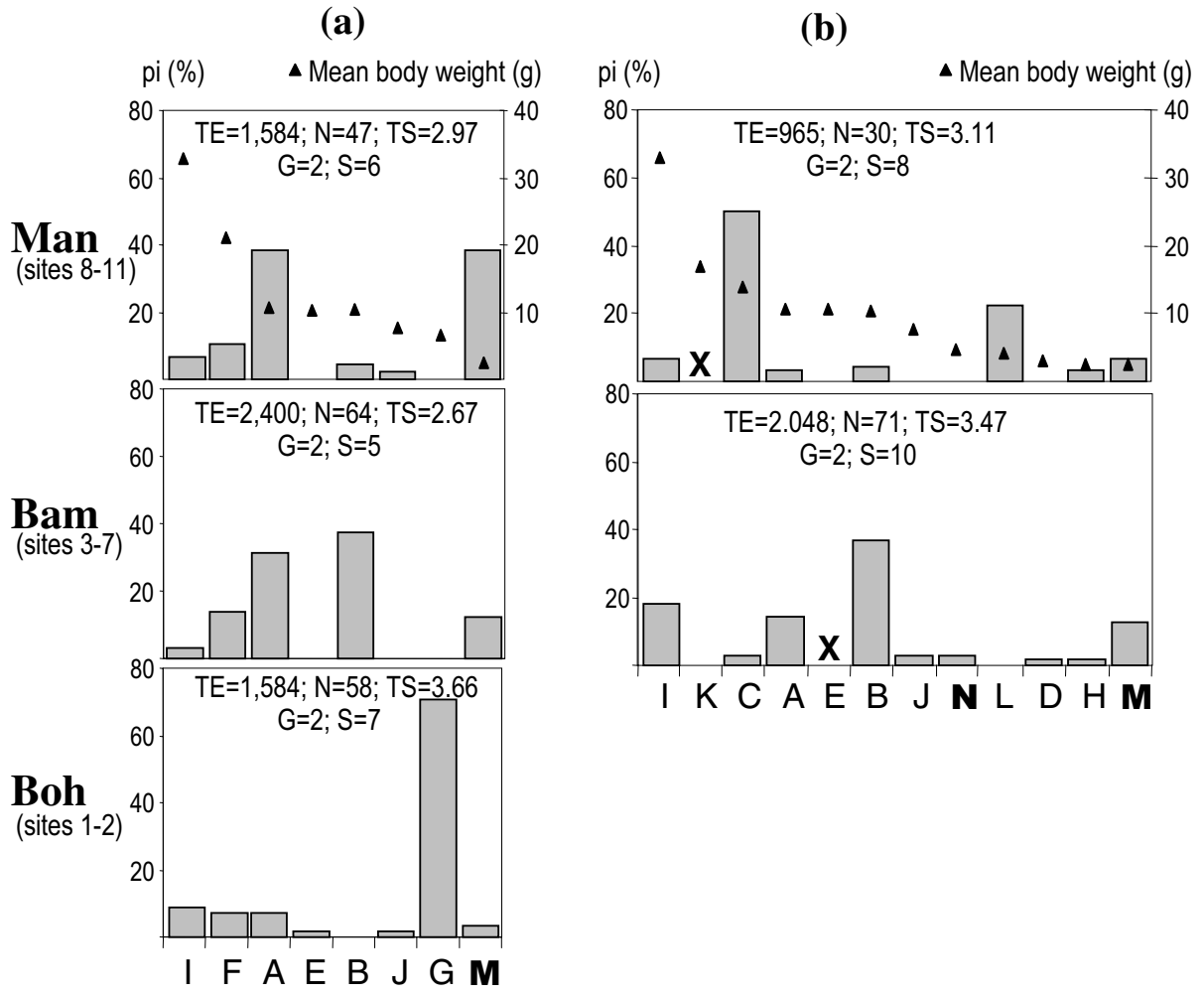

Fig. 2. – Pitfall trapping effort (TE); number of individuals (N), of genera (G) and of species (S) pitfall-trapped; trap success (TS) and distribution of relative abundance (pi) of the shrew species within (a) the gallery forests and (b) the surrounding savanna of the three main regions studied : Boh (Bohou), Bam (Bamingui-Bangoran) and Man (Manovo-Mara). Species codes (A-N) are defined in Table 2 and codes of the two *Suncus* species (M and N) are in bold. Species are ordered by decreasing mean body weight (as indicated by the triangles). Crosses indicate records by another mean than pitfall.

Community structure within the savanna

In the savanna zone of the two regions belonging to the Chad River basin, with a pitfall trapping effort of 3013 bucket-nights, 101 shrews (TS=3.35) representing two genera and ten species were recorded (Fig. 2b). Two additional species were collected by other means than pitfall trapping. The two genera (*Crocidura* and *Suncus*) were captured in each of the two regions. The number of species and the trap success were higher at Bamingui-Bangoran (S=10 and TS=3.47, respectively) than at Manovo-Mara (S=8 and TS=3.11). While the medium-sized *Crocidura* cf. *hildegardae* was dominant at Bamingui-Bangoran (pi=36.6%), the shrew community of Manovo-Mara was dominated by *C.* cf. *poensis* (pi=50%) of higher size.

Differences in the community structure between gallery forest and savanna

Species richness and trap success were higher in the two savanna habitats (S=12 and TS=3.35, respectively) than in the gallery forests (S=8 and T=3.04), despite a lower pitfall trapping effort (TE=3013). The difference in term of trap-success was mainly due to the capture of one additional species (*C.* cf. *poensis*), absent from the gallery forests and dominant at Manovo-Mara. *Suncus megalura* was captured only in the riparian savanna of the Bamingui-Bangoran region and the other species that were not captured in gallery forest are four savanna species (*C. fuscomurina, C. nanilla, C. turba* and *C. yankariensis*) and the problematic *C.* cf. *poensis*. The latter is taxonomically closely related to the savanna species *C. turba* and both belong to the poensis species complex, still in need of revision (Quérouil et al., in press). It could refer to a species different from the true

C. poensis, which could mainly occur in rainforest. For a given region, the shrew community structure varied between gallery forest and savanna, especially at Manovo-Mara where *C.* cf. *denti* and *S. infinitesimus* co-dominated in gallery forest (pi=38.3% each), while *C.* cf. *poensis* and *C. yankariensis* were the most abundant species in savanna (pi=50% and 23.3%, respectively). Whatever the habitat type the shrew community structure and the identity of the dominant species varied also between regions.

DISCUSSION

In order to test whether the natural gallery forests outside the Congolese rainforest could act as refuge for rainforest shrews, comparison of the shrew community within these galleries were made with two other communities in the northernmost part of the Congolese rainforest (Ray & Hutterer, 1996; Barrière et al., 2000; see Fig. 1 and Table 3), also situated in C.A.R. and within the West Central faunal region. In the Ngotto forest (Batouri River site), shrews were mainly pitfall-trapped (Barrière et al., 2000) while in Kongana, shrew remains were collected in carnivore scats (Ray & Hutterer, 1996). For the two communities combined, five genera and 20 species were collected (Table 3). In each of these two localities, rainforest species were the most numerous and represented altogether more than 88% of the whole collection.

TABLE 3

Comparison between the structure of shrew communities (pi, relative abundance) within gallery forests outside the Congolese rainforest and within the rainforest zone at two sites. "Forest I" means primary forest and "II" means secondary. When absent in the gallery forests, the presence of the species in the adjacent savanna is indicated by an "X" for each of the three regions. Region abbreviations : Boh (Bohou); Bam (Bamingui-Bangoran); Man (Manovo-Mara). Species in bold are known to occur within the rainforest zone. Habitat preferences (HP) : F, predominantly dense forest species; FS, species mainly occurring in transition zones such as secondary forest or forest-savanna mosaic; S, predominantly savanna species. Mean body weight (MBW) is given in grams.

				Within the Congolese rainforest		**Outside the rainforest**			
	Study location			**Batouri**	**Kongana**	**Boh**	**Bam**	**Man**	Total
	Main habitat type			Forest I	Forest I & II	Gallery forests			
	Period			Oct98 – Nov99	May92 – May94	May98 – Jul99			
	Mean of sampling			Pitfall	carnivore scats	Pitfall			
	Pitfall trapping effort (bucket-nights)			43,240	–	1,584	2,400	1,584	5,568
	Genus richness (G)			5	4	2	2	2	2
	Species richness (S)			18	16	7	5	6	8
	No of captures (N)			1,339	311	58	64	47	169
	Trap success (TS)			3.1		3.66	2.67	2.97	3.05
		HP	**MBW**						
	Sylvisorex johnstoni	F	2,9	**25.0**	**36.7**				
	Sylvisorex ollula	F	16,1	9.3	3.5				
	Crocidura nigrofusca	F	11,2	0.1	13.5				
	Sylvisorex konganensis	F	4,9	0.8	1.3				
	Paracrocidura schoutedeni	F	7,4	**17.6**	**24.1**				
	Congosorex verheyeni	F	7,1	1.8					
	Crocidura crenata	F	7,6	8.1					
	Crocidura dolichura	F	6,1	8.4	3.9				
	Suncus remyi	F	1,9	3.6	2.3				
	Crocidura batesi	F	16,0	11.1	3.2				
	Crocidura goliath	F	70,0	0.1	0.3				
	Sylvisorex pluvialis	F	5,0		1.0				
	Crocidura grassei	F	11,0	0.5					
	Crocidura poensis	F	14,0	2.1					
	Crocidura* cf. *m utesae	FS	16,1	0.3	2.3				
G	***Crocidura ludia***	FS	6,5	0.6	1.3	**70.7**			24.3
F	***Crocidura littoralis***	FS	21,0		2.3	6.9	14.1	10.6	10.7
B	***Crocidura* cf. *hildegardeae***	FS	10,3	0.1	1.3		**37.5**	4.3	15.4
A	***Crocidura* cf. *denti***	FS	10,5	0.9	2.9	6.9	**31.3**	**38.3**	24.9
I	***Crocidura olivieri***	FS	32,8	9.4	0.3	8.6	3.1	6.4	5.9
N	***Suncus megalura***	FS	4,5				x		x
M	*Suncus infinitesimus*	FS	2,5			3.5	12.5	**38.3**	16.6
J	*Crocidura roosevelti*	FS	7,6			1.7	x	2.1	1.2
E	*Crocidura lamottei*	S	10,5			1.7	x		0.6
D	*Crocidura fuscomurina*	S	3,0				x		x
H	*Crocidura nanila*	S	2,5				x	x	x
K	*Crocidura turba*	S	17,0					x	x
L	*Crocidura yankariensis*	S	4,4					x	x
C	*Crocidura* cf. *poensis*	S	14,0				x	x	x

In comparison, among the five genera occurring within the West Central region, only two (*Crocidura* and *Suncus*) were recorded in the gallery forests. A lower number of species was also recorded in the gallery forests (S=8). However, it is important to note that, at Batouri, when the cumulated pitfall trapping effort reached the value obtained at the northern galleries (5568 bucket-nights), four species had not been collected yet. None of the typi-

cal forest species of the genera *Sylvisorex, Paracrocidura, Suncus* and *Congosorex* was recorded in the gallery forests. *Suncus* was represented by *S. infinitesimus*, previously recorded from forest patches in forest-savanna mosaic, in eastern Congo and by *S. megalura*, which was only recorded within the savanna zone and is actually not a typical rainforest dweller but a widely distributed species (HUTTERER et al., 1987). Among the five *Crocidura* species recorded in both Congolese rainforest and gallery forest, all have ecological preferences directed towards open rainforest or forest patches within forest-savanna mosaic, and are medium or large sized. Three species, absent from the rainforest, were recorded within the gallery forests : *C. roosevelti* occurs at the margin of the rainforest in forest-savanna mosaic, and *C. lamottei* and *S. infinitesimus* occur only in savannas or in savanna-forest mosaic. Despite the absence of the typical forest shrew fauna within the gallery forests, it is noteworthy that *C. ludia*, which is listed as vulnerable (B1+2c) by the IUCN (HILTON-TAYLOR, 2000), was common at Bohou.

In Afro-tropical primary lowland rainforest, shrew communities, when surveyed by an adequate trapping protocol (i.e. pitfall traps with drift fence, NICOLAS et al., 2003) appear to be dominated by one of the smallest species, such as *Sylvisorex johnstoni* in West Central Africa (e.g. in Gabon : BARRIÈRE, 1997 ; GOODMAN et al., 2001 ; NICOLAS et al., 2004 ; in C.A.R. : BARRIÈRE et al., 2000 ; in Republic of Congo : BARRIÈRE, 1997 ; in Equatorial Guinea : LASSO et al., 1996 ; and in Cameroon : HUTTERER & SCHLITTER, 1996) ; or by *Crocidura obscurior* (3.6 g of mean body weight) in West Africa (Ivory Coast : BARRIÈRE et al., 1999 ; CHURCHFIELD et al., 2004). By contrast, in secondary forest or open habitats within the Congo River basin, the dominant shrews are usually larger, such as *C.* cf. *hildegardeae* (more than 10 g) in included savanna at Odzala National Park, Republic of Congo (Marc Colyn & Patrick Barrière, unpublished data) and at Ngotto forest, C.A.R. (BARRIÈRE et al., 2000), or such as *C. buettikoferi* (11 g) in cacao-coffee plantations included in the Taï National Park, Ivory Coast (BARRIÈRE et al., 1999). In the gallery forests of the Z.C.V., the tiny *S. infinitesimus* co-dominated (with *C.* cf. *denti*) the shrew community of Manovo-Mara and the small *C. ludia* highly dominated the community of Bohou. Nevertheless, it is noteworthy that the medium-sized *C.* cf. *hildegardeae* and *C.* cf. *denti* were co-dominant in Bamingui-Bangoran and that *C.* cf. denti was co-dominant (which *S. infinitesimus*) in Manova-Mara.

Among the 169 shrews, representing eight species, collected in gallery forests within three main regions, none of the typical rainforest shrews occurring within the Congo River basin was recorded. Similarly, no typical rainforest muroid rodent species was identified among a collection of 449 individuals, at the present state of analysis (Marc Colyn & Violaine Nicolas, unpublished data). The gallery forests harbour several plant, bird, primate and other larger mammal species, typical of the Congolese rainforest, suggesting that these galleries may presently act as refuge for these forest taxa. However, it is not the case for terrestrial small mammals. At first sight, these contrasting results are surprising. The observed differences may be attributed to distinct climatic and habitat characteristics as food resources, between the gallery forests and the Congolese rainforest. Being amongst the smallest mammals, shrews have high metabolic rates resulting in high energy requirements and water loss (CHURCHFIELD, 1990), especially the smallest species (VOGEL et al., 1981). These characteristics may be constraining life histories to a greater extent than occurs in larger mammals (SYMONDS, 1999) and could explain the differences observed between small mammals and larger ones. It is then possible that the typical rainforest shrews would not have survived in the gallery forests because the conditions would have been too dry and too hot in comparison to the more clement conditions of the Congo River basin.

Differences in food resources could also have an influence. Afro-tropical shrews, closely dependent on the understorey leaf litter, feed mainly on small arthropods. These shrews have a high level of food niche overlap and very small prey is of greatest importance to the smaller species (CHURCHFIELD et al., 2004 ; DUDU et al., in press). Therefore, shrews would be more dependent on the climatic conditions and food availability than larger mammals, and they could not have been able to survive in the warm and dry gallery forests in comparison to the Congolese rainforest. As previously suggested, central African endemic shrews are highly dependent on primary forest environments (HUTTERER et al., 1987). The unsuitability of these galleries to act as refuge for terrestrial small forest mammals could also be attributed to the small size of the patches, their peripheral location outside the present Congolese rainforest, more than 400 km from its margin, and the time elapsed since their isolation from the Congolese rainforest. This is in agreement with hypotheses which suggest that refuges could have been much larger, close to one another, on the margins of the rainforest zone and in the downstream zone of large rivers (HUTTERER et al., 1987 ; MALEY, 1996 ; DELEPORTE & COLYN, 1999).

CONCLUSION

Altogether, these findings support the hypotheses that Pleistocene refuges would have been composed of a network of forest patches within a forest-savanna mosaic rather than of small homogenous forest isolates and localised in the downstream zone of large rivers. The knowledge of the location and size of refuges is essential for the understanding of evolutionary scenarios. The refuges could probably not maintain the whole mammalian fauna, but rather a limited number of taxonomic units with suitable anatomy, physiology and ecological preferences. The knowledge of the history of tropical African floras and faunas will progress thanks to the multiplication of comparative phylogeographic studies (QUÉROUIL, 2001 ; QUÉROUIL et al., 2002 ; 2003) using relevant biological markers (COLYN & DELEPORTE, 2002a).

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REFERENCES

Barrière, P. (1997). Ecologie des Peuplements de Soricidae Forestiers d'Afrique Centrale : considérations nouvelles sur base de la méthode de piégeage Pitfall. *Report to the University of Rennes 1*, Rennes : 26 pp.

Barrière, P., P. Formenty, R. Hutterer, O. Perpète & M. Colyn (1999). Shrew community from Taï forest (Côte d'Ivoire); ecological vigil searching the Ebola virus reservoir. *Abstracts of the 8th International African Small Mammal Symposium*, MNHN, Paris : 57.

Barrière, P., V. Nicolas, R.K. Maro, G. Yangoundjara & M. Colyn (2000). Ecologie et structuration des peuplements de micromammiferes musaraignes et rongeurs. *ECOFAC-CEE report*, Libreville : 55 pp.

Bertaux, J., D. Schwartz, A. Vicens, A. Siffedine, H. Elenga, M. Mansour, A. Mariotti, M. Fournier, L. Martin, D. Wirrmann & M. Servant (2000). Enregistrement de la phase sèche d'Afrique centrale vers 3000 ans B.P. par la spectrométrie IR dans les lacs Sinnda et Kitina (sud-Congo). In : Servant & Servant-Vildary (eds), *Dynamique à long terme des écosystèmes forestiers intertropicaux*, Mémoires UNESCO, Paris : 43-49.

Boulvert, Y., (1986). *République centrafricaine, carte phytogéographique*. Editions de l'ORSTOM, Paris : 131 pp.

Churchfield, S. (1990). *The natural history of shrews*. Christopher Helm (ed), London : 175 pp.

Churchfield, S., P. Barrière, R. Hutterer & M. Colyn (2004). First results on the feeding ecology of sympatric shrews (Insectivora : Soricidae) in the Tai National Park, Ivory Coast. *Acta Theriologica,* 49(1) : 1-15.

Christy, P. (1999). La République Centrafricaine, carrefour biogéographique. *Canopée, Bulletin sur l'Environnement en Afrique Centrale,* 14 : 6.

Colyn, M. (1991). L'importance zoogéographique du bassin du fleuve Zaïre pour la spéciation : le cas des primates simiens. *Ann. Mus. R. Afr. Centr.*, Tervuren, Belgique : 264.

Colyn, M. (1999). Un nouveau statut biogéographique pour l'Afrique centrale. *Canopée, Bulletin sur l'Environnement en Afrique Centrale,* 14 : 3-5.

Colyn, M., & P. Deleporte (2002a). Marqueurs biologiques en biogéographie historique : problèmes de taxonomie, de distribution et de filtre écologique. *Biosystema,* 20 : 41-48.

Colyn, M., & P. Deleporte (2002b). Biogeographic analysis of central African forest Guenons. In : Glenn & Cords (eds), *The Guenons : Diversity and Adaptation in African Monkeys.*, Kluwer Academic/Plenum Publishers, New-York : 61-78.

Colyn, M., A. Gauthier-Hion & W. Verheyen (1991). A reappraisal of the paleoenvironment history in Central Africa : evidence for a major fluvial refuge in the Zaire basin. *J. Biogeogr.,* 18 : 403-407.

Deleporte, P., & M. Colyn (1999). Biogéographie et dynamique de la biodiversité : application de la PAE aux forêts planitiaires d'Afrique centrale. *Biosystema,* 17 : 37-43.

Dudu, A., S. Churchfield & R. Hutterer (in press). Community structure and food niche relationships of coexisting rainforest shrews in the Masako Forest, north-eastern Congo. In : Merritt, Churchfield, Hutterer & Sheftel (eds), *The Biology of the Soricidae II*, Carnegie Museum of Natural History Special Publication.

ECOFAC online : (http ://www.ecofac.org).

ECOFAC (2001). Composante RCA, Projet de développement des zones cynégétiques villageoises. Rapport d'activités juillet-décembre 2001 (http ://www.ecofac.org/Composantes/ZonesCynegetiquesVillageoises.htm). *ECOFAC-CEE report*, Libreville : 116-137.

Fay, M. (1988). Faunal monkey populations in the Central African Republic : the northern limits. A census in Manovo-Gounda-St. Floris National Park. *Mammalia,* 52 : 57-74.

Goodman, S.M., R. Hutterer & P.R. Ngnegueu (2001). A report on the community of shrews (Mammalia : Soricidae) occurring in the Minkebe Forest, northeastern Gabon. *Mammal. Biol.,* 66 : 22-34.

Haffer, J. (1969). Speciation in neotropical birds. *Science,* 165 : 131-137.

Hilton-Taylor, C. (2000). 2000 IUCN Red List of Threatened Species. IUCN, Gland, Switzerland and Cambridge, UK : xviii + 61 pp.

Hutterer, R., E. Van der Straeten & W.N. Verheyen (1987). A checklist of the shrews of Rwanda and biogeographical considerations of African Soricidae. *Bonn. Zool. Beiträge,* 38 : 155-172.

Hutterer, R. (1993). Order Insectivora. In : Wilson & Reeder (eds), *Mammal species of the world, a taxonomic and geographic reference*, second edition, Washington, D.C. : 69-130.

Hutterer, R., & D.A. Schlitter (1996). Shrews of the Korup National Park, Cameroon, with the description of a new *Sylvisorex* (Mammalia : Soricidae). *Spec. Publ. Mus. Texas Tach. Univ.,* : 57-66.

Lasso, C., R. Hutterer & A. Rial (1996). Records of shrews (Soricidae) from Equatorial Guinea, especially from Monte Alen National Park. *Mammalia,* 60 : 69-76.

Leal M. (2000). Microrefugia, small scale ice age forest remnants. In : Robbrecht & Degreef (eds), *Abstracts XVIth AETFAT Congress. Scripta Bot. Belg.* : 3.

Maley J. (1987). Fragmentation de la Forêt Dense Humide Africaine et extension des biotopes montagnards au Quaternaire récent : nouvelles données polliniques et chronologiques. Implications paléoclimatiques et biogéographiques. *Palaeoecology of Africa* 18 : 307-334.

Maley, J. (1996). The African rain forest - main characteristics of changes in vegetation and climate from the Upper Cretaceous to the Quaternary. *Proc. R. Soc. Edinburgh* 104B : 31-73.

Maley, J. (2001). La destruction catastrophique des forêts d'Afrique centrale survenue il y a environ 2500 ans exerce encore une influence majeure sur la répartition actuelle des formations végétales. *Syst. Geogr. Pl.*, 71 : 777-796.

Maley, J., & P. Brenac (1998). Vegetation dynamics, palaeoenvironments and climatic changes in the forests of west Cameroon during the last 28,000 years. *Rev. Palaeobot. Palyno*., 99 : 157-188.

Nicolas, V., P. Barrière & M. Colyn (2003). Impact of removal pitfall trapping on the community of shrews (Mammalia : Soricidae) in two African tropical forest sites. *Mammalia,* 67 : 133-138.

Nicolas, V., P. Barrière, S. Guimondou & M. Colyn (2004). Variabilité structurale des peuplements forestiers de rongeurs (Muridae) et musaraignes (Soricidae) dans les Monts Doudou, Gabon. In : Fischer (ed), *A floral and faunal inventory of Monts Doudou : Gabon with reference to elevation variation*, Proceedings of the California Academy of Sciences, Memoir 28, San Francisco : 107-127.

Quérouil, S. (2001). Intérêts et limites de l'approche moléculaire pour aborder la biogéographie et la spéciation :

quelques exemples chez les mammifères d'Afrique tropicale. *Ph.D. thesis*, University of Rennes 1, France : 310 pp.

QUÉROUIL, S., R. HUTTERER, P. BARRIÈRE, M. COLYN, J.C. KERBIS PETERHANS & E. VERHEYEN (2001). Phylogeny and evolution of African Shrews (Mammalia : Soricidae) inferred from 16s rRNA sequences, *Mol. Phylogenet. Evol.,* 20(2) : 185-195.

QUÉROUIL, S., M. COLYN, E. VERHEYEN & P. DELEPORTE (2002). De la phylogéographie comparée à la biogéographie historique : l'exemple de quelques mammifères forestiers d'Afrique centrale. *Biosystema* 20, Systématique et Biogéographie : 131-140.

QUÉROUIL, S., E. VERHEYEN, M. DILLEN & M. COLYN (2003). Patterns of diversication in two African forest shrews : *Sylvisorex johnstoni* and *Sylvisorex ollula* (Soricidae, Insectivora) in relation to paleo-environmental changes. *Mol. Phylogenet. Evol.,* 28 : 24-37.

QUÉROUIL, S., P. BARRIÈRE, M. COLYN, R. HUTTERER, A. DUDU, M. DILLEN & E. VERHEYEN (in press). A molecular insight into the systematics of African *Crocidura* (Crocidurinae, Soricidae) using 16s rRNA sequences. In : MERRITT, CHURCHFIELD, HUTTERER & SHEFTEL (eds), *The Biology of the Soricidae II*, Carnegie Museum of Natural History Special Publication.

RAY, J.C. & R. HUTTERER (1996). Structure of a shrew community in the Central African Republic based on the analysis of carnivore scats, with the description of a new *Sylvisorex* (Mammalia : Soricidae). *Ecotropica,* 1 : 85-97.

SYMONDS, M.R.E. (1999). Life histories of the Insectivora : the role of phylogeny, metabolism and sex differences. *J. Zool. London,* 249 : 315-337.

TÉLLO, J.L. (2000). Inquiétante recrudescence du braconnage des éléphants dans le nord de la centrafrique. *Canopée, Bulletin sur l'Environnement en Afrique Centrale,* 17 : 11-12.

VOGEL, P., M. GENOUD & H. FREY (1981). Rythme journalier d'activité chez quelques Crocidurinae africains et européens (Soricidae, Insectivora). *Rev. Ecol. (Terre Vie),* 35 : 97-108.

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The fibrovascualar ring : A synapomorphy of hystricognath Rodentia newly described in *Petromus typicus* and *Octodon degus*

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ABSTRACT. Hystricognathi is a higher monophyletic taxon within Rodentia that is supported particularly by characters of early ontogeny and placentation. Since the original findings are based on a small sample of species, further information on character distribution is desirable. The present paper provides new insight into the morphology of one of the most significant characters in two additional species of Hystricognathi, i.e. *Petromus typicus* A. SMITH, 1831 and *Octodon degus* MOLINA, 1782. In both species an arterial ring within the inverted yolk sac splanchnopleura that is associated with a network of capillaries is present throughout pregnancy. Consequently, the existence of the so called "fibrovascular ring" is confirmed for these species and distributional data suggest that it can be regarded as a synapomorphic feature of Hystricognathi. Thus, two of the three original diagnostic characters of Hystricognathi are now confirmed for a larger set of taxa.

KEY WORDS : Rodentia, Hystricognathi, phylogeny, ontogeny, fetal membrane structures, yolk sac vessels, sinus terminalis, fibrovascular ring.

INTRODUCTION

Hystricognathi is a well established taxon within Rodentia (TULLBERG, 1899/1900; SIMPSON, 1945; EISENBERG, 1981; LUCKETT & HARTENBERGER, 1985, 1993; WILSON & REEDER, 1993; MCKENNA & BELL, 1997; NEDBAL et al., 1994; HUCHON et al., 1999, 2000). It is supported as a monophylum particularly by characters of early ontogeny and placentation as summarised by PATRICK LUCKETT in 1985 and widely accepted by the scientific community. However, these important findings are based on only 8 species of Hystricognathi, which have been more or less well studied and often not including detailed descriptions of the morphological context (cf. LUCKETT, 1985; MOSSMAN, 1987). Moreover, members of several larger groups of Hystricognathi are not included in that sample (see below). Thus, further investigations are necessary in order to reveal the distribution of fetal membrane characters. Accordingly, in the last couple of years investigation of fetal membrane structures in two additional species of Hystricognathi have been conducted, based on breeding groups of the South African dassie rat (*Petromus typicus*) and the South American degu (*Octodon degus*). Both belong to subgroups of Hystricognathi that have been suggested to represent most probably basal offshoots of the African and South American hystricognaths, respectively (see MESS, 1999a for background information). Thus, investigation of their fetal membrane structures is essential to a fuller understanding of the evolutionary differentiation of Hystricognathi. Especially for *Petromus*, it is only recently that information on placentation (e.g., MESS, 1999b, 2001, 2003) or even basic data on reproductive biology (MESS, 2002, 2005; MESS et al., 2002) were obtainable. Publications on fetal membrane structure resulting from this work focussed on the structural organisation of the chorioallantoic placenta (cf. MESS, 2003), whereas other structures such as the yolk sac are currently under investigation. At present, one of the original defining characters of Hystricognathi is found in the two investigated species : the subplacenta as a distinct region within the chorioallantoic placenta (MESS, 2003). The present work provides insights into another one of the defining characters of Hystricognathi according to LUCKETT'S review, i.e. the fibrovascular ring (following the nomenclature of PERROTTA, 1959) or capillary band (according to LUCKETT & MOSSMAN, 1981). This structure represents a network of capillaries within the inverted yolk sac splanchnopleura that is associated with a ring-like artery. It is known only for Hystricognathi. The main focus herein is a description of the morphology of the ring system in the two species. Finally, its evolutionary and phylogenetic significance is discussed too.

MATERIAL AND METHODS

To reveal the occurrence of the fibrovascular ring and the associated ring-like artery, either vascular injections of the yolk sac vessels or else histological sections have to be conducted. The later method is more often used, and thus the present study is based on histological serial sections of *Petromus typicus* and *Octodon degus*. All material was obtained from the breeding groups of both species, housed at the Humboldt-University, Berlin. Information on the examined stages is given in the text or

else is provided in MESS (2003). The study focuses on that stages that includes the ring in total in order to follow the course of the vessels and to reveal if the fibrovascular ring and the artery possess a ring-like structure. In some of the later stages that are also used for this study, only one half of the placenta was prepared for light microscopy, whereas the other parts have been used for electron microscopy or other applications. Thus, in some of these cases additional information is derived from manually prepared specimens. The histological sections have been analysed with Zeiss Axioskop or Axioplan microscopes and the structures of interest have been documented by using a Camera Lucida. The reconstruction of character evolution was done on the basis of pre-existing cladograms by using MacClade (Version 4.0)[1]. Since opinions on the phylogenetic relationships of Hystricognathi to other Rodentia varies, members of each of the main rodent subgroups are included as out-groups, and two independently established trees (derived from NEDBAL et al., 1994, 1996, and MCKENNA & BELL, 1997) are used (see discussion). Accordingly, the stem species pattern of Rodentia (= the character set of the last common ancestor of all rodents) is reconstructed as a first step towards recognising the evolutionary transformations on the stem lineage of Hystricognathi. Data on the character distribution in relevant taxa is summarised in Table 1, and the results of the MacClade analysis (including character treatment, CI and RI values) are given by Fig. 3.

TABLE 1

Distribution of the fibrovascular ring system within the inverted yolk sac splanchnopleura and its development in rodent species and some members of other eutherian orders, derived from the literature and own material. Short names (*) are given for each species, which are used to demonstrate the results of the analysis in Fig. 3.

Character I – Ring-like artery : 1 = absent, 2 = present.
Character II – Network of capillaries : 1 = absent, 2 = present.
Character III – Extent of the ring system : 1 = absent, 2 = not prominent, 3 = prominent.

Species	(*)	I	II	III	Main citation
Petromus typicus	Pet	2	2	2	MESS (2003), present study
Octodon degus	Oct	2	2	2	MESS (2003), present study
Cavia porcellus	Cav	2	2	3	Several studies, see MOSSMAN (1987); own material
Erethizon dorsatum	Ere	2	2	3	PERROTTA (1959)
Myocastor coypus	Myo	2	2	3	HILLEMANN & GAYNOR (1961)
Chinchilla lanigera	Chin	2	2	3	TIBBITS & HILLEMANN (1959)
Dasyprocta spec.	Dasy	2	2	3	BECHER (1921a, b); MIGLINO (pers. comm.)
Thryonomys swinderianus	Thry	2	2	3	ODUOR-OKELE & GOMBE (1982, 1991)
Hystrix africaeaustralis	Hyst	2	2	3	LUCKETT & MOSSMAN (1981)
Bathyergus janetta	Bath	2	2	3	LUCKETT & MOSSMAN (1981)
Rattus norvegicus	Rat	1	1	1	e.g. BRIDGEMAN (1948); own material
Mus musculus	Mus	1	1	1	e.g. THEILER (1972); own material
Jaculus jaculus	Jac	1	1	1	KING & MOSSMAN (1974)
Aplodontia rufa	Aplo	1	1	1	HARVEY (1959a)
Citellus tridecemlineatus	Cite	1	1	1	e.g. MOSSMAN & WEISFELDT (1939)
Sciurus vulgaris	Sci	1	1	1	e.g. SCHOOLEY (1934); own material
Geomys bursarius	Geo	1	1	1	MOSSMAN & HISAW (1940); MOSSMAN & STRAUSS (1963)
Castor canadensis	Cast	1	1	1	WILLEY (1912); FISCHER (1971)
Pedetes capensis	Ped	1	1	1	FISCHER & MOSSMAN (1969); OTIANG'A-OWITI et al. (1992)
Oryctolagus cuniculus	Ory	1	1	1	MOSSMAN (1926, 1987); own material
Ochotona spec.	Och	1	1	1	HARVEY (1959b)

RESULTS

1. The fibrovascular ring in Petromus typicus

In the youngest investigated stage of *Petromus typicus* of about 5 weeks of pregnancy, an arterial ring is situated within the yolk sac splanchnopleura where the latter is attached to the chorioallantoic placenta (Figs 1a-d). According to the inverted nature of the yolk sac in Hystricognathi and other rodents, the yolk sac vessels are situated on the inner side, whereas the yolk sac endoderm is on the outer side in close vicinity to the uterus (Figs 1a-d). The artery possesses two branches running in the yolk sac splanchnopleura along the umbilical cord (Figs 1b, c). At the outer border of the chorioallantoic placenta the branches are fused to each other (Figs 1a, d), assuming a ring-like structure of the artery. From the arterial ring, smaller arteries branch out in their way to supply the extended area of the yolk sac splachnopleura. In Fig. 1c, such an offshoot of the arterial ring is given on the right side. The artery is accompanied by a dense network of capillaries, the fibrovascular ring or capillary band (Figs 1a-d). As, for instance, in the guinea pig, the ring-like artery is intermingled within these capillaries.

[1] The number of characters is too small to develop an own phylogeny, e.g. by applying Paup.

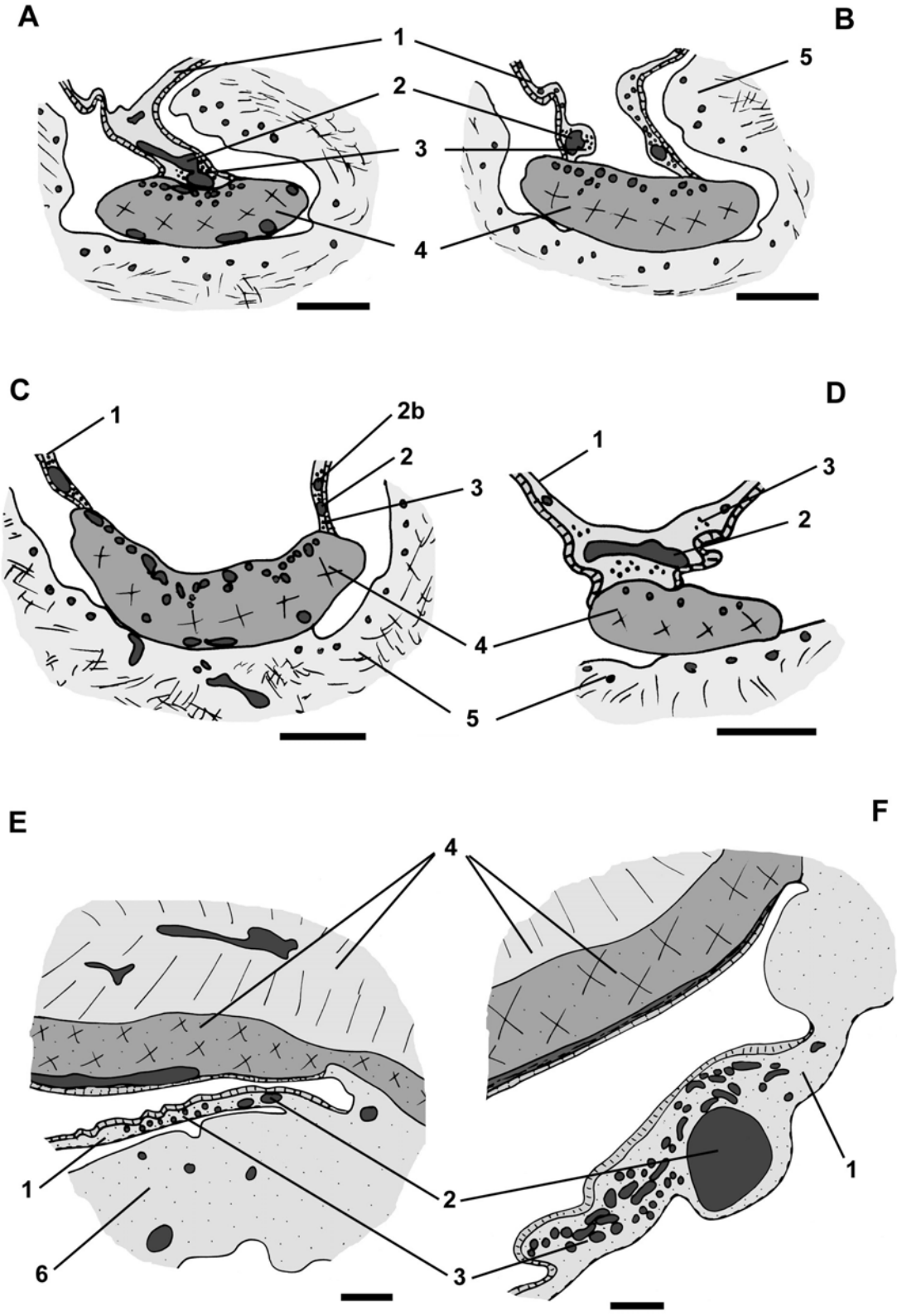


Fig. 1. – The fibrovascular ring in different ontogenetic stages of the African *Petromus typicus*.
A-D : about 5 weeks of pregnancy, early placental differentiation stage
(corresponding to *Petromus* 26 in MESS (2003)).
E : about 7 to 8 weeks of pregnancy, mid gestation
(corresponding to *Petromus* 19b).
F : about 12 weeks of pregnancy, near-term stage
(corresponding to *Petromus* 1).
*Abbrevations see Fig. 2.

In older stages of *Petromus* of either 7 to 8 weeks of pregnancy (mid gestation) as well as in several near-term stages (about 12 weeks of pregnancy), the arterial system is in a similar position (Figs 1e, f). Most of the investigated material allows no clear decision about whether it is ring shaped. However, at least in one near-term stage, a ring-like structure of the artery and the associated fibrovascular ring or capillary band is clearly established. A ring-like structure of the artery also appears in a macroscopically prepared specimen. The later stages are characterised by the following : In the mid-term stage a modestly prominent artery is situated within the yolk sac splanchnopleura near to the attachment of the chorioallantoic placenta (Fig. 1e). It is in close association with the relatively small, undifferentiated network of capillaries (Fig. 1e). This capillary band (or fibrovascular ring) is more laterally extended along the yolk sac splanchnopleuric surface than in the earlier stage. The artery and its offshoots are interrelated to this network of capillaries as described above. Since in the mid-term stage an infolding of the yolk sac splanchnopleura begins, it should be assumed that the above described arterial system does not reach far laterally to that region of the splanchnopleura (cf. Fig. 1e). Finally, in near-term stages the artery is more distant to the chorioallantoic placenta than in former stages (Fig. 1f). Also in these term stages the artery is accompanied by the network of capillaries. Although the distinctness and lateral extension of the capillaries in every specimen varies within the yolk sac splanchnopleura, the capillary band or fibrovascular ring is, even in near-term stages, not very prominent at all (Fig. 1f shows a portion of the object with a quite well differentiated capillary network). Laterally the artery and the associated fibrovascular ring now reach to that region of the yolk sac splanchnopleura where the infolding took place (Fig. 1f).

2. The fibrovascular ring in Octodon degus

As in *Petromus*, *Octodon* has an arrangement of an artery and a network of capillary in the inverted yolk sac splanchnopleura throughout pregnancy. The first indication of the structures of interest can be noticed in an early stage of 25 to 26 days of pregnancy, where the vascularisation of the yolk sac splanchnopleura begins[2]. In the next stage of 35 days of pregnancy, the arterial system can clearly be recognised (Fig. 2a). The artery is quite small and is situated very near to the attachment of the yolk sac splanchnopleura to the chorioallantoic placenta. It possesses a ring-like structure, and supplies smaller arterial vessels that run along the surface of the yolk sac splanchnopleura (Fig. 2a). The accompanying capillaries are likewise relatively small and not markedly differentiated, but clearly intermingled with the artery (Fig. 2a). The artery and the related capillary band or fibrovascular ring is in some distance from the region where the infolding of the yolk sac splanchnopleura begins (Fig. 2a).

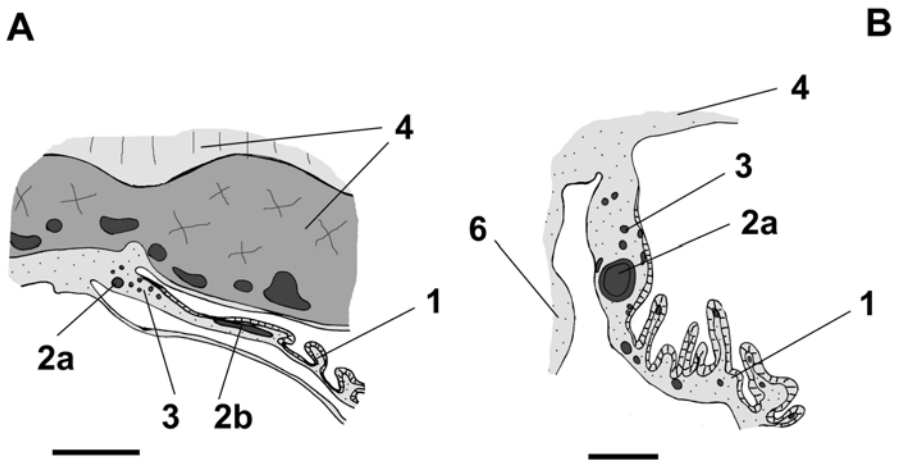


Fig. 2. – The fibrovascular ring in the South American hystricognath rodent *Octodon degus*.
A : about 5 weeks of pregnancy, placental differentiation stage (corresponding to *Octodon* 17 in MESS (2003)).
B : late pregnancy, 64 days (corresponding to *Octodon* 10).

Abbreviations in Figs 1-2 (scale bar = 1 mm) :
1 : yolk sac splanchnopleura
2a : ring-like artery in the splanchnopleura
2b : lateral offshoot of the artery
3 : capillary band or fibrovascular ring associated with the artery
4 : chorioallantoic placenta
5 : uterus
6 : umbilical cord

[2] However, the specimen was fixed only with formaldehyde in total, and thus the structures are not very distinctly preserved, and thus a detailed description of this stage is impractical.

In older stages of *Octodon* of either 64 days of pregnancy or 84 days (near-term stage), a quite similar picture is recognisable : The artery is still small, as well as the associated capillary band which is only formed by a limited number of individual capillaries (Fig. 2b). These structures are situated very near to the attachment to the chorioallantoic placenta even in advanced developmental stages (Fig. 2b). In macroscopically studied material similar in age, a ring-like structure of the artery is likely.

DISCUSSION

In *Petromus typicus* as well as in *Octodon degus* an artery within the inverted yolk sac splanchnopleura associated with a network of capillaries, the capillary band or fibrovascular ring is established throughout pregnancy. Both species possess ring-like arteries : In the youngest stage of *Petromus*, a nearly complete ring-like structure of the artery appears to be present since its two branches are fused to each other in the histological serial section. At least in one of the near-term stages as well as in a manually prepared specimen, a ring-like structure is present, suggesting that it is present throughout pregnancy. In *Octodon* the ring-like structure of the artery and its capillary network occurs in histological sections of the 5 week old stage and in manually prepared specimens of various ages. In both species the fibrovascular ring is situated near the attachment site towards the chorioallantoic placenta, distinct from the villous splanchnopleura that has differentiated during later ontogeny. However, in all investigated serial sections of near-term stages, the capillary band is not as prominent as is the case in late pregnancy stages of other Hystricognathi such as *Cavia* or *Hystrix* (see Table 1).

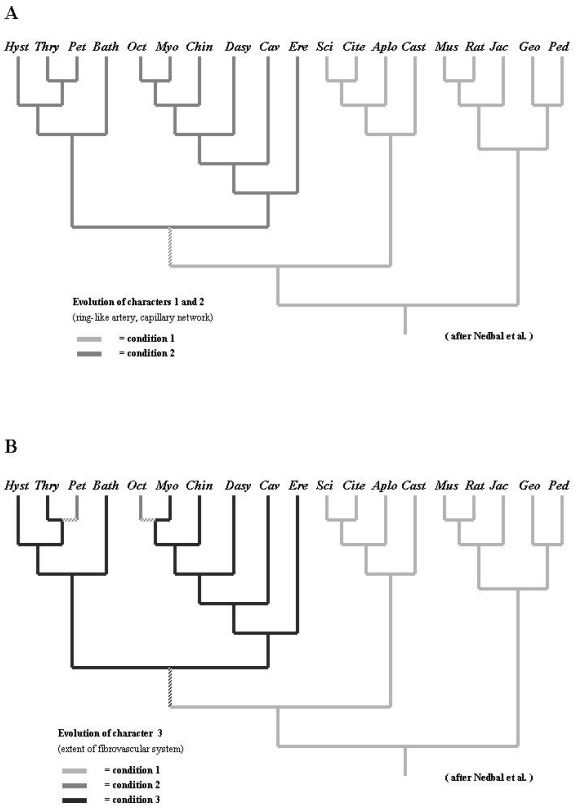
A fibrovascular ring was first described as a dense network of capillaries that is accompanied by a complete or nearly complete ring-like artery supplied by the yolk sac artery in the guinea pig *Cavia porcellus* by RUTH JACKSON, later MOSSMAN (R.J. MOSSMAN, 1927, cited after LUCKETT & MOSSMAN, 1981; MOSSMAN, 1987). Hence, this ring-like structure within the yolk sac splanchnopleura surrounds the attachment of the umbilical cord and radiates into finer vessels that supply the yolk sac surface. Following the original discovery, the ring system was noticed in illustrations derived from former studies on fetal membranes in *Cavia*, although not mentioned in the text (relevant citations in MOSSMAN, 1987). Moreover, the existence of such an arterial ring system appears to be present in other members of Hystricognathi that have been investigated in regard to their fetal membrane structures, i.e. in *Erethizon dorsatum* (PERROTTA, 1959 : "Fibrovascular ring"), *Chinchilla lanigera* (TIBBITTS & HILLEMANN, 1959 : "Sinus terminalis", network of capillaries and multiple anastomosis), *Myocastor coypus* (HILLEMANN & GAYNOR, 1961 : "Sinus terminalis"), *Hystrix africaeaustralis* and *Bathyergus janetta* (LUCKETT & MOSSMAN, 1981 : "Sinus terminalis or arterial circle with capillary band), *Thryonomys swinderianus* (ODUOR-OKELO & GOMBE, 1982, 1991 : "Fibrovascular ring", ODUOR-OKELO, pers. comm), and *Dasyprocta azarae* (cf. MOSSMAN, 1987, original description by BECHER, 1921a, b). Finally, in the material of some newly described South American species the fibrovascular ring system seem also be present, e.g. in *Kerodon rupestris* and *Agouti paca* (MIGLINO, pers. comm.). In all these species, the arterial ring and its associated capillary band are characteristically similar to that of the guinea pig. Moreover, as far as described by the authors, it reached laterally at least to the beginning of the villous region of the yolk sac splanchnopleura. The only difference within the taxa sample is the fact, that the ring system is not fully circular in some species such as *Hystrix* (LUCKETT & MOSSMAN, 1981). *Petromus* and *Octodon* clearly fit into the described pattern, and thus the presence of the fibrovascular ring is established for the species investigated herein. In non-hystricognath rodent taxa, an arterial and capillary ring system has not been found in similar position so far (see Table 1, e.g. WILLEY, 1912; MOSSMAN, 1926, 1987; SCHOOLEY, 1934; MOSSMAN & WEISFELD, 1939; MOSSMAN & HISAW, 1940; BRIDGEMAN, 1948; HARVEY, 1959a, b; MOSSMAN & STRAUSS, 1963; FISCHER & MOSSMAN, 1969; FISCHER, 1971; THEILER, 1972; KING & MOSSMAN, 1974; LUCKETT, 1985; OTIANG'A-OWITI et al., 1992).

The functional meaning of this structure is completely unknown, as well as its origin during vascularisation of the yolk sac splanchnopleura or the possible evolutionary precursors (LUCKETT & MOSSMAN, 1981; MOSSMAN, 1987). However, the presence of the fibrovascular ring is essential for phylogeny, since it is one of three synapomorphies of Hystricognathi given by LUCKETT in 1985, especially as characters that are uniquely derived in African and American hystricognath rodents (LUCKETT & MOSSMAN, 1981). With the discovery of these characters, the long-lasting dispute about the independent development of Hystricognathi from different continents was settled at least in the mid 1980's (LUCKETT & HARTENBERGER, 1985). Information on the distribution of the fibrovascular ring within hystricognaths is now accessible for a larger set of taxa, i.e. more than ten species altogether comprising also members of subgroups that are supposed to represent basal offshoots.

A reconstruction of character evolution was carried out by applying MacClade on the basis of pre-existing hypotheses of rodent systematic. Though several molecular phylogenies are available (e.g., HUCHON et al., 2000 (nuclear gene, i.e. vWF); ADKINS et al., 2001 (combined analysis on several nuclear and rRNA genes)), most of these studies cannot be used, because they consider small taxa samples that usually do not include *Petromus* (or even *Octodon*). Thus, following MESS (2003), a cladogram based on 12S-rRNA genes (NEDBAL et al., 1994, 1996) is chosen in preference to reconstruct character evolution. Moreover, an independently established, morphology-based classification (MCKENNA & BELL, 1997) is considered too. Rodentia and members of Lagomorpha as an additional out-group are used in this tree, because the evolution of yolk sac characters is not resolved by considering only rodents (see MESS, 2003)[3]. In both of the cladograms under consideration, only those species can be utilised for which sufficient

[3] MCKENNA & BELL (l.c.) present Lagomorpha and Macroscelidea as nearest relatives of Rodentia. The results from the analysis do not change, if a member of Macroscelidea had been chosen instead of the lagomorphs.

data about fetal membrane structures are available, resulting in a restricted number of species and relationships compared to the original trees (see Table 1 and Fig. 3)[4]. Characters 1 and 2 are respectively the presence or absence of the ring-like artery and the capillary network. Additionally, the extent of the fibrovascular ring system is included (character 3), i.e. the dorsolateral extent of the capillary band and the intermingled artery in the yolk sac splanchnopleura based on a subjective impression. The characters are treated as unordered. Accordingly, the presence of the ring-like artery (character 1) and the associated network of capillaries (character 2) in the yolk sac splanchnopleura resulted as evolutionary transformations towards Hystricognathi in both of the underlying trees, and thus the fibrovascular ring system appears to be a synapomorphic or derived character state for hystricognaths (Figs 3a, c). Since two independently established trees support the same character polarity, the presumed character evolution appears relatively stable. Finally, in regard to character 3, the molecular tree indicated a prominent fibrovascular ring system in the stem species pattern of Hystricognathi as a derived condition within Rodentia, and independent transformations from the hystricognath stem species pattern towards the inconspicuous conditions in the newly investigated *Petromus* and *Octodon* (Fig. 3b). In contrast, the morphology-based tree allows no establishment of this character polarity within hystricognaths (Fig. 3d). Thus, the available results only tentatively suggest that *Petromus* and *Octodon* have (independently) reduced the extent of their fibrovascular ring system, although the presumed character polarity appears not to be very stable.



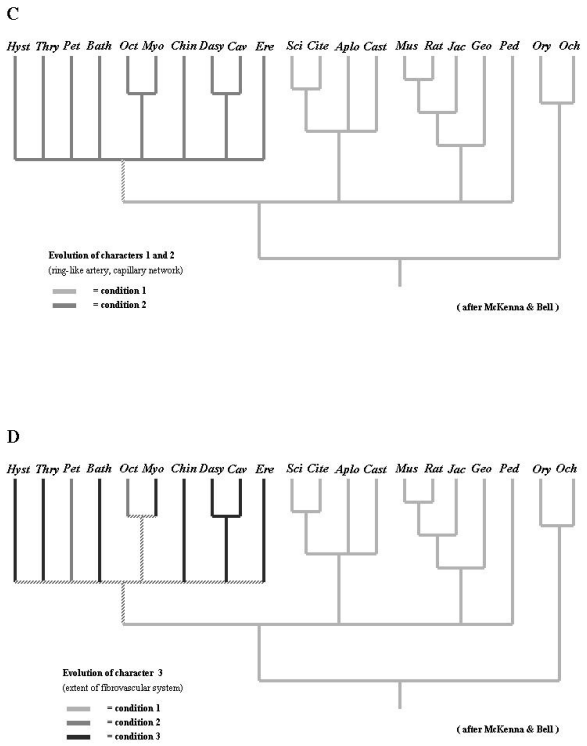


Fig. 3. – Results of the MacClade analysis on the two selected cladograms, i.e. a molecular phylogeny (NEDBAL et al., 1994, 1996) and morphology-based relationships (MCKENNA & BELL, 1997). The characters are treated as unordered. CI = 0.8, RI = 0.96 in both trees. See Table 1 for abbreviations and full names of the selected taxa.
A : Evolution of characters 1 and 2 after NEDBAL et al.
B : Evolution of character 3 after NEDBAL et al.
C : Evolution of characters 1 and 2 after MCKENNA & BELL
D : Evolution of character 3 after MCKENNA & BELL

CONCLUSION

In conclusion, the fibrovascular ring is revealed for a larger set of taxa within hystricognaths and the distributional data suggest that it can be regarded as homologous within hystricognaths and as a synapomorphic feature of that group. The present findings consolidate LUCKETT'S hypothesis. Thus, up to now two of the three defining characters of Hystricognathi – the fibrovascular ring and the subplacenta – have been confirmed for more taxa. Very early ontogenetic stages of *Petromus* and *Octodon* have not been studied so far, and thus, no information is available on the third synapomorphy of Hystricognathi according to LUCKETT (1985), the primary interstitial implantation.

ACKNOWLEDGEMENTS

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[4] Compared to the above mentioned study (MESS, 2003), some more Hystricognathi are included, and some non-hystricognath species are omitted (the data are more homogenous than that of the chorioallantoic placenta).

thank the organisers for carrying out this stimulating meeting as well as for the chance to publish symposiums proceedings. The establishment of the breeding groups of *Petromus typicus* and *Octodon degus* as well as the gathering and processing of placental material took place at the Humboldt-University, Berlin within the Institute of Systematic Zoology of the Museum of Natural History. Consequently, I would like to thank the director of that institution, Prof. U. Zeller, and all colleagues that are involved in the different stages of this project. Prof. H. Hoch and her team enabled the use of MacClade. Moreover, I am grateful to Manfred Ade for comments on earlier versions of the manuscript, and to Patrick Luckett for discussions on the *Petromus* material during his stay in Berlin a few years ago. Finally, I want to thank Jason Dunlop for helping with the English, and an unknown referee for helpful comments on a former version of the manuscript.

LITERATURE CITED

ADKINS, R.M., E.L. GELKE, D. ROWE & R.L. HONEYCUTT (2001). Molecular Phylogeny and divergence time estimates for major rodent groups : evidence from multiple genes. *Mol. Biol. Evol*., 18 : 777-791.

BECHER, H. (1921a). Die Entwicklung des Mesoplacentariums und die Placenta bei Agouti (*Dasyprocta azarae* Schl.). *Z. Anat. Entw.-gesch.*, 61 : 337-364.

BECHER, H. (1921b). Der feinere Bau der reifen Plazenta von Agouti (*Dasyprocta azarae* Schl.). *Z. Anat. Entw.-gesch*., 61 : 439-454.

BRIDGEMAN, J. (1948). A morphological study of the development of the placenta of the rat. I. An outline of the development of the placenta of the white rat. *J. Morph*., 83 : 61-85.

EISENBERG, J.F. (1981). *The mammalian radiation. An analysis of trends in evolution, adaptation, and behaviour.* Athone Press, London.

FISCHER, T.V. (1971). Placentation in the American beaver (*Castor canadensis*). *Am. J. Anat*., 131 : 159-184.

FISCHER, T.V. & H.W. MOSSMAN (1969). The fetal membranes of *Pedetes capensis*, and their taxonomic significance. *Am. J. Anat*., 124 : 89-116.

HARVEY, E.B. (1959a). Placentation in Aplodontidae. *Am. J. Anat*., 105 : 63-89.

HARVEY, E.B. (1959b). Placentation in Ochotonidae. *Am. J. Anat*., 104 : 61-85.

HILLEMANN, H.H. & A.I. GAYNOR (1961). The definitive architecture of the placentae of Nutria, *Myocastor coypus* (Molina). *Am. J. Anat*., 109 : 299-317.

HUCHON, D., F.M.CATZEFLIS & E.J.P. DOUZERY (1999). Molecular Evolution of the Nuclear von Willebrand Factor Gene in Mammals and the Phylogeny of Rodents. *Mol. Biol. Evol.*, 16 : 577-587.

HUCHON, D., F.M. CATZEFLIS & E.J.P. DOUZERY (2000). Variance of molecular datings, evolution of rodents and the phylogenetic affinities between Ctenodactylidae and Hystricognathi. *Proc. R. Soc. Lond*. B, 267 : 393-402.

KING, B.F. & H.W. MOSSMAN (1974). Fetal membranes and unusual giant cell placenta of the jerboa (*Jaculus*) and jumping mouse (*Zapus*). *Am. J. Anat*., 140 : 405-432.

LUCKETT, W.P. (1985). Superordinal and intraordinal affinities of rodents. Developmental evidence from the dentition and placentation. In : LUCKETT & HARTENBERGER (eds), *Evolutionary Relationships among Rodents*, Plenum Press, New York, NATO ASI-Series 92 : 227-276.

LUCKETT, P. & J.-L. HARTENBERGER (1985). Evolutionary relationships among rodents : comments and conclusions. In : LUCKETT & HARTENBERGER (eds), *Evolutionary Relationships among Rodents*, Plenum Press, New York, NATO ASI-Series 92 : 685-712.

LUCKETT, W.P. & J.-L. HARTENBERGER (1993). Monophyly or Polyphyly of the Order Rodentia : Possible Conflict Between Morphological and Molecular Interpretations. *J. Mamm. Evol*., 1 : 127-147.

LUCKETT, W.P. & H.W. MOSSMAN (1981). Development and phylogenetic significance of the fetal membranes and placenta of the African hystricognathous rodents, *Bathyergus* and *Hystrix*. *Am. J. Anat*., 162 : 266-285.

MCKENNA, M.C. & S.K. BELL (1997). *Classification of mammals above the species level*. Columbia University Press, New York.

MESS, A. (1999a). The rostral nasal skeleton of hystricognath rodents : evidence on their phylogenetic interrelationships. *Mitt. Mus. Naturk. Berlin, Zool. Reihe*, 75 : 19-35.

MESS, A. (1999b). Plazentation von *Petromus typicus*, ein Beitrag zur Reproduktionsbiologie und evolutiven Differenzierung der Hystricognathi. *Courier Senckenberg*, 215 : 153-157.

MESS, A. (2001). Evolutionary differentiation of placental organisation in hystricognath rodents. In : DENYS, GRANJON & POULET (eds), *African Small Mammals*, IRD Éditions, collection Colloques et séminaires. Paris : 279-292.

MESS, A. (2002). *Petromus typicus* : reproductive biology of a poorly known animal. *Research Committee Newsletter*, 8 : 38-40.

MESS, A. (2003). Evolutionary transformations of chorioallantoic placental characters in Rodentia with special reference to hystricognath species. *J. Exp. Zool*., 299A : 78-98.

MESS, A. (2005) : Felsenratte. In : GANSLOßER, U. (ed), *Die Sozialsysteme der Säugetiere*, Filander Verlag, Fürth : 156-158.

MESS, A., J. PINT & K. FAUST (2002). Ontogenetic differentiation in *Petromus typicus* : a basis for more detailed interpretation of results on ultrasonic approaches in a precocial rodent. *Advances in Ethology*, 37 : 145.

MOSSMAN, H.W. (1926). The rabbit placenta and the problem of placenta transmission. *Am. J. Anat*., 37 : 433-497.

MOSSMAN, H.W. (1987). *Vertebrate Fetal Membranes. Comparative Ontogeny and Morphology, Evolution, Phylogenetic Significance, Basic Function Research Opportunities.* Rutgers University Press, New Brunswick, New Jersey.

MOSSMAN, H.W. & F.L. HISAW (1940). The fetal membranes of the pocket gopher illustrating an intermediate type of rodent membrane formation. I. From the unfertilized tubal egg to the beginning of the allantois. *Am. J. Anat*., 66 : 367-391.

MOSSMAN, H.W. & F. STRAUSS (1963). The fetal membranes of the pocket gopher illustrating an intermediate type of rodent membrane formation. II. From the beginning of the allantois to term. *Am. J. Anat*., 113 : 447-477.

MOSSMAN, H.W. & L.A. WEISFELDT (1939). The fetal membranes of a primitive rodent, the thirteen-striped ground squirrel. *Am. J. Anat*., 64 : 59-109.

MOSSMAN, R.J. (1927). *The yolk-sac placental circulation of the guinea-pig.* Thesis, University of Wisconsin.

NEDBAL, M.A., M.W. ALLARD & R.L. HONEYCUTT (1994). Molecular systematics of hystricognath rodents : Evidence from the mitochondrial 12S rRNA gene. *Mol. Phylogenet. Evol.*, 3 : 206-220.

NEDBAL, M.A., R.L. HONEYCUTT & D.A. SCHLITTER (1996). Higher-level systematics of rodents (Mammalia, Rodentia) : Evidence from the mitochondrial 12S rRNA gene. *J. Mamm. Evol.*, 3 : 201-237.

ODUOR-OKELO, D. & S.G. GOMBE (1982). Placentation in the cane rat (*Thryonomys swinderianus*). *Afr. J. Ecol*., 20 : 49-66.

ODUOR-OKELO, D. & S.G. GOMBE (1991). Development of the foetal membranes in the cane rat (*Thryonomys swinderianus*) : a re-interpretation. *Afr. J. Ecol*., 29 : 157-167.

OTIANG'A-OWITI, G.E., D. ODOUR-OKELO & S.G. GOMBE (1992). Foetal membranes and placenta of the springhare (*Pedetes capensis larvalis* Hollister). *Afr. J. Ecol*., 30 : 74-86.

PERROTTA, C.A. (1959). Fetal membranes of the Canadian porcupine, *Erethizon dorsatum*. *Am. J. Anat*., 130 : 35-59.

SIMPSON, G.G. (1945). The principles of classification and a classification of mammals. *Bull. Am. Mus. Nat. Hist*., 85 : 1-350.

SCHOOLEY, J.P. 1934. Early development in some Sciuridae. *J. Morph.,* 56 : 477-511.

THEILER, K. (1972). *The House Mouse. Development and Normal Stages from Fertilisation to 4 Weeks of Age.* Springer, New York.

TIBBITTS, F.D. & H.H. HILLEMANN (1959). The development and histology of the chinchilla placenta. *J. Morph*., 105 : 317-366.

TULLBERG, T. (1899/1900). *Ueber das System der Nagethiere : eine phylogenetische Studie*. Akademische Buchdruckerei, Uppsala.

WILLEY, A. (1912). Foetal membranes of the American beaver (*Castor canadensis*). *Zool. Jahrb*. (Suppl 15), 2 : 191-218.

WILSON, D.E. & D.M. REEDER (1993). *Mammal species of the world. A taxonomic and geographic reference*. Smithsonian Institution Press, Washington, London.

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Barn owl pellets : a useful tool for monitoring small mammal communities?

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ABSTRACT. Monthly fluctuations in the diet of Barn owl *Tyto alba* were compared to prey availability in a typical South African dry sandy highveld grassland over a 12 month period. Mice, shrews, bats, birds and insects were all major prey items, and their contribution in pellets fluctuated significantly over months. Barn owl proved to be very efficient samplers of the small mammal prey group : not only was the owl more successful than museum personnel in sampling the variety of species present during a specific time of year, but peaks in prey utilization were also more characteristic of actual fluctuations than that found by traps. Owl pellet analysis is a valuable asset during small mammal monitoring studies, and is especially useful for sampling small mammal indicator species during environmental impact assessments. However, owl pellet analysis should never be seen as an alternative for small mammal trapping when small mammal community structure is the focus of study.

KEY WORDS : Barn owl, small mammal, monitoring, sampling method

INTRODUCTION

Lately, small mammal communities have been used as indicators of habitat integrity (see AVENANT, 2000a, 2003; AVENANT & KUYLER, 2002; AVENANT & WATSON, 2002). A growth curve (Fig. 1) has been postulated for a number of animal & plant groups (see WANG et al., 1999), whereby highest species richness increase with succession (= primary productivity) up to a point of climax, and then decrease to a point where equilibrium is reached. Species number fluctuates around this point until disturbance takes place. Depending on the measure and speed of disturbance the number of species for the specific animal group may follow the curve backwards, with highest species numbers found at intermediary disturbance, and lowest species number found at/after extreme disturbance. "Relatively few ruderal species dominate when disturbances are frequent, and relatively few highly competitive species dominate when disturbances are rare; intermediate levels of disturbance allow succession to proceed but limit the ability of competitive species to dominate the community" (VALONE & KELT, 1999). The number of microhabitats and primary productivity is also high at the point of climax, and able to sustain a number of individuals from different species. The data of a number of longer term small mammal studies in southern Africa can be fitted to this curve (e.g. ROWE-ROWE & LOWRY, 1982; ROWE-ROWE, 1995; FERREIRA & VAN AARDE, 2000), while our relatively short-term studies (AVENANT, 2000a, b; KUYLER pers. comm.; AVENANT & KUYLER, 2002; AVENANT & WATSON, 2002), where small mammal communities were correlated with the abundance of pioneer plant species and/or ecological value of the veld in the Free State province, indicate that a similar curve can be expected. The latter studies have also indicated that small mammal Shannon-diversity and Evenness (E_{var}) may be good indicators of ecosystem integrity, as it increases from (a) to (b) in Fig. 1. Generalist species (or species with a wide habitat tolerance) were generally found to dominate small mammal numbers on the lower part of the curve, with the opposite true for specialist species, which increase in number towards the end of the curve. Together, these findings led to the idea that the direct monitoring of small mammals be used as a relatively quick and inexpensive method of indicating ecological disturbance/habitat integrity, and therefore a useful tool for wildlife managers and environmental consultants.

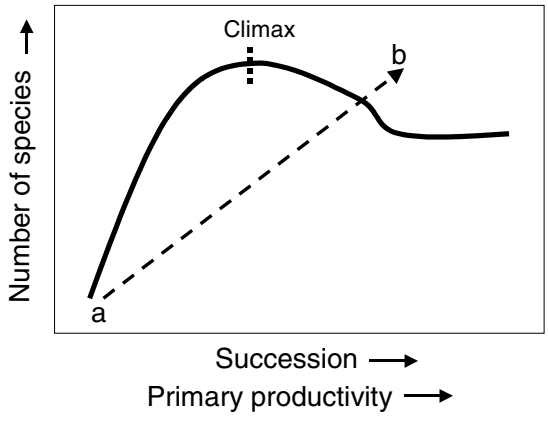

Fig. 1. – Correlation between number of small mammal species and succession / primary productivity. See text for a description of letters a, b.

Identifying small mammal remains from animal scats and pellets is an indirect method of monitoring small mammals. In the past it has been a useful tool for animal-ecologists and wildlife managers : it does not only reflect the hunting and feeding behaviour of the predator, but are

also useful for studying the systematics, geographical distribution, population ecology and craniology of prey animals. Fossil remains derived from owl pellets have also made an important contribution in the reconstruction of palaeo-environments (see DAVIS, 1959; AVERY, 1982, 1987, 1991, 1992, 1999).

In the present study the indirect method of the analysis of modern Barn owl, *Tyto alba affinis* Blyth, 1862, pellets were compared to our direct method of monitoring small mammals, and the relevance of these results to the study of habitat integrity considered.

MATERIAL AND METHODS

Study area

Between March 1998 and September 2000 more than 400 pellets of the Southern African Barn Owl, *Tyto alba*, were collected on a daily basis from a single locality at Florisbad Research Station (28°46'S; 26°04'E), central interior of South Africa. The vegetation is typical Dry Sandy Highveld Grassland (Veld type 37 - LOW & REBELO, 1996). Mean annual precipitation in this summer rainfall area is *c.* 450mm, and mean daily maximum and minimum temperatures ranges from *c.* 31°C and 14°C in January to *c.* 16°C and -1°C in July (WEATHER BUREAU, 1986).

Fresh pellets were individually placed in paper bags, air-dried and later teased apart. Large, easily diagnosed fragments of prey were macroscopically identified while hair, teeth and feathers were identified under a stereo microscope at 25x or 50x magnification. Prey items were identified to species level where possible by comparing undigested remains with a reference collection and from published results, e.g. scales on hair imprints (KEOGH, 1983 a, b) and tooth form (DE GRAAFF, 1981; PERRIN, 1982; BOWLAND & BOWLAND, 1989).

Both *percentage volume* (a prey item's percentage contribution to total volume ingested) and *percentage occurrence* (a percentage of the number of pellets in which a prey item was present) of prey items in pellets were determined, and an *Importance Value* calculated (IV = *percentage volume* x *percentage occurrence* / 100). The computer programme Statistica for Windows (Statsoft Inc., 1995) was used to do the statistical analyses. Analysis of Variance (ANOVA) tests were used to detect inter-group differences. The 95% level ($p<0.05$) was regarded as statistically significant for all tests.

Small mammals were sampled during late-summer and late-autumn at the six most diverse habitats in the Florisbad Research Station grounds :

(1) Exotic *Kikuju* sp. grass & *Eucalyptus* sp. trees (28°46.052'S; 26°04.248'E); (2) Open eroded area (28°46.044'S; 26°04.303'E); (3) Low bushes on post-climax grassland (28°45.893'S; 26°04.243'E); (4) Vegetation (mostly sedges) around a swampy area (28°46.045'S; 26°04.268'E); (5) "Open" *Themeda triandra* grassland (28°46.039'S; 26°04.352'E); (6) "Dense" *Themeda triandra* grassland (28°45.910'S; 26°04.186'E). Sites 1 and 2 were considered the most influenced by man, and sites 5 and 6 the least.

The standardized method prescribed to EIA consultants working in the Free State grassland (AVENANT, 2000b; FERREIRA & AVENANT, 2003) were used to sample small mammal communities : One hundred snap traps were placed per transect. These were spaced 5m apart and left open, checked and re-baited in the early morning and late afternoon for four consecutive days and nights. Bait used was a mixture of peanut butter, rolled oats, sunflower oil and *marmite* (yeast extract). Rodents and shrews trapped were sexed, weighed, measured, dissected and study skins and skulls deposited in the National Museum (Bloemfontein, South Africa) collection. Trap success (or percentage success) is the number of small mammals captured per 100 trap nights. Variety is the number of species found, while diversity, calculated using the Shannon index (MAGURRAN, 1988), is a measure of both the number of species and equality of representation of the individuals of all species.

To increase our species list, 100 PVC live traps (on separate, 10 m distant parallel transects), 10 pitfall traps (15 cm diameter, 20 cm deep; at random trap stations on each transect), and spades (to search in disused termitaria) were also used.

RESULTS & DISCUSSION

The main prey items (i.e. contributing > 40% to the volume of the majority of pellets in which it occurs) were : mice (mean monthly IV = 68.0), birds (IV = 1.4), insects (IV = 0.7; orders Coleoptera, Lepidoptera, Orthoptera & Mantodea), shrews (IV = 0.4) and bats (IV = 0.01) (Table 1). Molerat and plant material were present in < 0.5% of pellets. No reptile remains were found. All main prey items, except bats, fluctuated significantly ($p<0.05$) over months (Fig. 2). The fluctuation pattern of mice, the major prey item in the diet of the Barn owl, did not simply follow their densities (density significantly highest in late-autumn/early-winter, and lowest just before the start of their breeding season at the end of winter : see AVENANT, 2000a, b), but were, nevertheless, more accurate than our small mammal trapping over the past six years in indicating real densities (sampling with traps have, among others, been found to be influenced by differences in age group structure and the availability of natural food). The other prey items generally follow the inverse pattern of mice, being highest from *c*. October to May.

TABLE 1

Mean monthly Percentage Occurrence, Percentage Volume, and Importance Value (IV) of prey items of the southern Barn Owl *Tyto alba* at Florisbad Research Station, 1998 – 2000.

Prey item	% Occurrence	% Volume	IV
Mice	85.4	79.6	68.0
Shrews	10.7	4.1	0.4
Molerats	0.5	6.1	0.03
Bats	2.3	0.6	0.01
Birds	13.4	10.6	1.4
Insects	14.2	4.6	0.7
Plants	0.3	0.1	0.0003

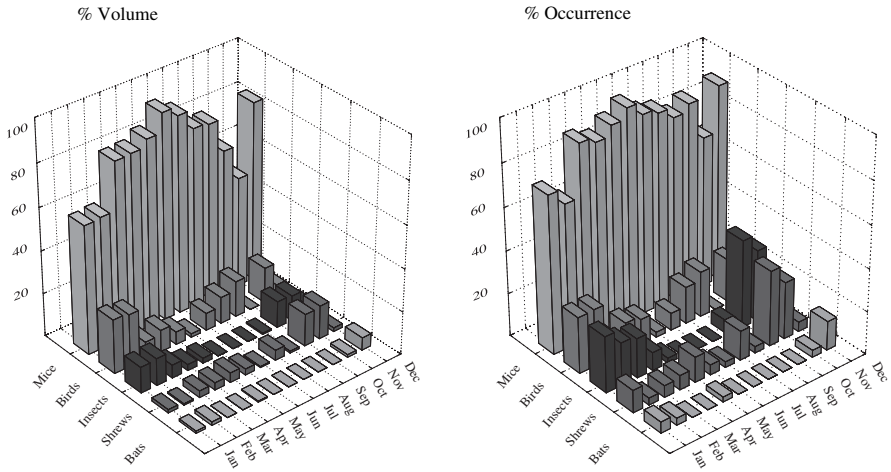

Fig. 2. – Monthly fluctuations of the main prey items in the diet of southern African Barn owl *Tyto alba* at Florisbad Research Station.

The nocturnal small mammal species *Mastomys coucha* and *Tatera* spp. contributed by far the highest percentage to the volume of prey ingested (Fig. 3). From September to April, however, the crepuscular *Rhabdomys pumilio* and diurnal *Otomys irroratus* became more important as prey. *Does this mean that the owl forages at different times during the warmer and colder months, or is it that the crepuscular and diurnal prey become inactive earlier during the winter days as soon as the temperature drops?*- no answer could be found in the literature.

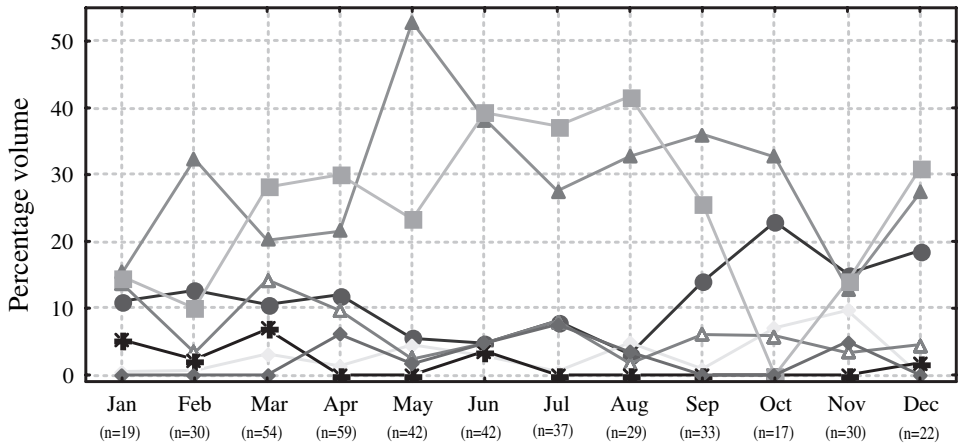

Fig. 3. – Monthly fluctuations of the main small mammal prey species (i.e. contributing > 3% to the volume of pellets in at least one month) in the diet of southern African Barn owl *Tyto alba* at Florisbad Research Station.

, R. pumilio; , M. coucha; , C. cyanea; , O. irroratus; M. albicaudata; , Tatera spp.; , R. rattus

In the present study, analysis of owl pellets proved useful when determining small mammal species present in this grassveld ecosystem. Despite its preference for some species, the Barn owl nevertheless sampled more species than our extensive trapping efforts indicated (Table 2). The presence of *Tatera brantsi*, *Myosorex varius*, and the red listed *Mystromys albicaudatus*, and difficult to sample *Saccostomus campestris* and *Desmodillus auricularis* were only indicated by its presence in owl scats. Although the owl may forage outside of the Florisbad Research Station grounds, all species found in owl pellets are expected to occur within the grounds. Also, four other species sampled by the owl could not be found by traditional trapping methods (see Table 2). This effective sampling of Barn owls has been shown in a number of other studies (e.g. HAPPOLD & HAPPOLD, 1986; DENYS et al., 1999; BA et al., 2000; GRANJON et al., 2002). As in our small mammal studies (see AVENANT, 2003), however, the owl has found the "scarcer" c. 15 percent of the total number of small mammal species sampled only in the late autumn - early winter months, while more than 25 percent of species were not preyed upon in the spring months.

The multimammate mouse *Mastomys coucha*, as well as species richness and diversity, has been used as an indicator of disturbance (see AVENANT, 2000a, b; AVERY, 1991, 1992). In the relatively disturbed habitats at Florisbad this mouse has been found to dominate in four of the six habitats sampled by museum personnel. It was also a

TABLE 2

Terrestrial small mammal species sampled by the southern African Barn owl *Tyto alba* versus small mammal species sampled by personnel of the National Museum. X, sampled by traps; x, sampled by alternative methods (see text).

Small mammal species	Owl	Personnel
Rhabdomys pumilio	X	X
Mastomys coucha	X	X
Otomys irroratus	X	X
Mystromys albicaudatus	X	
Saccostomus campestris	X	
Desmodillus auricularis	X	
Tatera leucogaster	X	X
Tatera brantsi	X	
Mus minutoides	X	X
Mus musculus	X	x
Rattus rattus	X	x
Myosorex varius	X	
Crocidura cyanea	X	X
Suncus varilla	X	x
Cryptomys hottentotus	X	x
Total number of species	**15**	**10**

major prey item of the owl. Commensal species, such as the house mouse and house rat, have being used to describe changes in vegetation / presence of man in palaeontological times. In the present study these two species contributed throughout the year to owl diet – a low contribution, with no significant difference between months or seasons ($p>0.1$) – but were not found in our traps.

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REFERENCES

AVENANT, N.L. (2000a). Small mammal community characteristics as indicators of ecological disturbance in the Willem Pretorius Nature Reserve, Free State, South Africa. *S. Afr. J. Wildl. Res.,* 30 : 26-33.

AVENANT, N.L. (2000b). Terrestrial small-mammal diversity in Korannaberg Conservancy, Free State, South Africa. *Navors. Nas. Mus., Bloemfontein.*16(4) : 69-82.

AVENANT, N.L. (2003). The use of small-mammal community characteristics as an indicator of ecological disturbance in the Korannaberg Conservancy. In : SINGLETON, HINDS, KREBS & SPRATT (eds), *Rats, Mice & People : Rodent Biology and Management*, ACIAR Monograph No 96.

AVENANT, N.L. & P. KUYLER (2002). Small mammal diversity in the Maguga area, Swaziland. *S. Afr. J. Wildl. Res.,* 32 : 101-108.

AVENANT, N.L. & J.P. WATSON (2002). Mammals recorded in the Sandveld Nature Reserve, Free State Province, South Africa. *Navors. Nas. Mus., Bloemfontein.* 18(1) : 1-12.

AVERY, D.M. (1982). Micromammals as palaeoenvironmental indicators and an interpretation of the late quarternary in the southern Cape Province, South Africa. *Ann. S. Afr. Mus.,* 85 : 183-374.

AVERY, D.M. (1987). Late Pleistocene coastal environment of the Southern Cape Province of South Africa : micromammals from Klasies River mouth. *J. Archaeol. Sci.,* 14 : 405-421.

AVERY, D.M. (1991). Micromammals, owls and vegetation change in the Eastern Cape Midlands, South Africa, during the last millennium. *J. Archaeol. Sci.,* 20 : 357-369.

AVERY, D.M. (1992). Man and/or climate? Environmental degradation and micromammalian community structure in South Africa during the last millennium. *S. Afr. J. Science,* 88 : 483-489.

AVERY, D.M. (1999). A preliminary assessment of the relationship between trophic variability in southern African Barn Owls *Tyto alba* and climate. *Ostrich,* 70(3&4) : 179-186.

BA, K., L. GRANJON, R. HUTTERER & J-M. DUPLANTIER (2000). Les micromammifères du Djoudj (Delta du Sénégal) par l'analyse du régime alimentaire de la chouette effraie, *Tyto alba*. *Bonn. Zool. Beitr.,* 49 : 31-38.

BOWLAND, A.E. & J.M. BOWLAND (1989). An identification to rodent prey in carnivore scats and pellets. *Lammergeyer,* 40 : 8-9.

DAVIS, D.H.S. (1959). The Barn owl's contribution to ecology and palaeoecology. *Ostrich sup.,* 3 : 144-153.

DE GRAAFF, G. (1981). *The Rodents of Southern Africa*. Butterworth & Co., Pretoria.

DENYS, C., W. CHITAUKALI, J.K. MFUNE, M. COMBREXELLE & F. CACCIANI (1999). Diversity of small mammals in owl pellet assemblages of Karonga district, northern Malawi. *Acta zool. Cracov.,* 42 : 393-396.

FERREIRA, S.M. & N.L. AVENANT (2003). Influences of trap-spacing on descriptors of hypothetical small mammal communities in grasslands at Tussen-die-Riviere Nature Reserve. *Navors. Nas. Mus., Bloemfontein.* 19 : 21-30.

FERREIRA, S.M. & R.J. VAN AARDE (2000). Maintaining diversity through intermediate disturbances : evidence from rodents colonizing rehabilitating coastal dunes. *Afr. J. Ecol*., 38 : 286-294.

GRANJON, L., C. BRUDERER, J.F. COSSON, A.T. DIA & F. COLAS (2002). The small mammal community of a coastal site of south-west Mauritania. *Afr. J. Ecol.,* 40 : 10-17.

HAPPOLD, C.D. & M. HAPPOLD (1986). Small mammals of Zomba Plateau, Malawi, as assessed by their presence in pellets of the Grass owl, *Tyto capensis*, and by live-trapping. *Afr. J. Ecol*., 24 : 77-87.

KEOGH, H.J. (1983a). A photographic reference system of the microstructure of the hair of Southern African Cricetidae and Muridae. *S. Afr. J. Wildl. Res*., 13 : 1-51.

KEOGH, H.J. (1983b). A photographic reference system of the microstructure of the hair of southern African bovids. *S. Afr. J. Wildl. Res.,* 13 : 89-131.

LOW, A.B. & A.G. REBELO (1996). *Vegetation of South Africa, Lesotho and Swaziland.* Department of Environmental Affaires and Tourism. Pretoria.

MAGURRAN, A.E. (1988). *Ecological diversity and its measurement*. Cambridge University Press, Cambridge.

PERRIN, M.R. (1982). Prey specificity of the Barn owl, *Tyto alba,* in the Great Fish River valley of the Eastern Cape Province. *S. Afr. J. Wildl. Res.,* 12(1) : 14-25.

ROWE-ROWE, D.T. (1995). Small-mammal recolonization of a fire-exclusion catchment after unscheduled burning. *S. Afr. J. Wildl. Res.,* 25(4) : 133-137.

ROWE-ROWE, D.T. & P.B. LOWRY (1982). Influence of fire on small-mammal populations in the Natal Drakensberg. *S. Afr. J. Wildl. Res.,* 12 : 130-139.

VALONE, T.J. & D.A. KELT (1999). Fire and grazing in a shrub-invaded arid grassland community : independent or interactive ecological effects? *J. Arid. Env.,* 42 : 15-28.

WANG, G., Z. WANG, Q. ZHOU & W. ZHONG (1999). Relationship between species richness of small mammals and primary productivity of arid and semi-arid grasslands in north China. *J. Arid. Env.,* 43 : 467-475.

WEATHER BUREAU (1986). *Climate of South Africa. Climate statistics up to 1984.* Government Printer, Pretoria.

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Feeding biology of the dassie-rat *Petromus typicus* (Rodentia, Hystricognathi, Petromuridae) in captivity

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ABSTRACT. We examined the feeding biology of the poorly known dassie-rat *Petromus typicus*. External morphology indicates that the digging for soil-inhabiting invertebrates as food is unlikely. Animals in captivity refuse to eat insect larvae and data from field studies indicate that invertebrates play no major role with regard to the intake quantity. Observations on jaw movements and occlusion patterns of the cheek teeth indicate that *Petromus* is not restricted to high-fibre plant matter as food. This matches the catholic diet of *Petromus* in captivity and in the wild, where e.g. flowers and fruits are consumed when available. The rooted and moderately hypsodont cheek teeth suggest limited adaptation to abrasive plant material in comparison to other grass feeding hystricognaths. However, captive specimens consume high fibrous graminoid material during all activity phases, even when energetically more rewarding food is available. This suggests that fibre is an important food component. The stomach has no proventriculus or similar structure. Therefore, fermentation of plant matter in that region and/or rumination is unlikely. The caecum is large and haustrated, indicating the ability to process cellulose by micro-organisms. The morphology of the proximal colon indicates the presence of the so-called *colon separating mechanism* (CSM). It is therefore likely that the animals are able to produce vitamin and protein-rich faeces. This is confirmed by the occurrence of coprophagy by *Petromus*. The great variety of food sources hints at the ability of *Petromus* to cope with unstable environments, as is the case in xeric areas.

KEY WORDS : Rodentia, Hystricognathi, *Petromus*, feeding behaviour, nutrition, digestive system, coprophagy, rumination.

INTRODUCTION

African hystricognath rodents are well known as porcupines (Hystricidae), cane rats (Thryonomyidae), as well as by the group of subterranean species of mole rats (Bathyergidae). In contrast, the monotypic family Petromuridae (TULLBERG, 1899/1900; cf. MCKENNA & BELL, 1997; WILSON & REEDER, 1993) and its only member, the dassie-rat or noki *Petromus typicus* A. SMITH, 1831 (Fig. 1a), is less well known. *Petromus* is endemic to the Southern African Subregion, confined to the arid to semi-arid zone in the southernmost parts of Angola, in Namibia, and in the north-western part of the Cape Province in RSA (SKINNER & SMITHERS, 1990; COETZEE, 2002). It appears to be the geologically oldest rodent inhabitant of the Namib desert (MEESTER, 1965). It lives in rocky habitats, for instance in the crevices of the kopjes in the Namibian escarpment (SKINNER & SMITHER, 1990). Accordingly, *Petromus* possesses features regarded as adaptations for living in rock crevices, i.e. a flattened skull and flexible ribs (VAUGHAN et al., 2000; see also TULLBERG, 1899/1900; ELLERMAN, 1940; NOWAK, 1999).

Hystricognathi, including *Petromus*, differ conspicuously from other rodents : Derived characters (apomorphies) are associated with their reproduction which is characterised by a k-selective or precocial strategy (MESS et al., 2001). They are mainly herbivorous. Since *Petromus* is often suggested to have retained a large number of plesiomorphic conditions of Hystricognathi (cf. MESS, 1999a), this species is important for reconstructing the evolution of mammals in Africa. Particularly, according to the dassie-rats limited distribution and tolerance to xeric conditions, it could serve as a model for understanding how mammals use strategies to cope with the increasing aridity of the Southern African Subregion.

Data on *Petromus* is remarkably "few" : Only some basic information on their natural habitat, nutrition and reproduction is available (e.g., WITHERS et al., 1980; DE GRAAFF; 1981; SKINNER & SMITHERS, 1990; COETZEE, 1983, 2002; NOWAK, 1999), including a few field studies (WITHERS, 1979, 1983; GEORGE, 1981; GEORGE & CROWTHER, 1981; COETZEE 2002; RATHBUN & RATHBUN, this volume). It had been assumed that *Petromus* is able to ruminate (COETZEE, 1983). According to GEORGE (1981) the diet is dominated by graminoids and the species is considered a herbivore (see also COETZEE, 1983). However, one report found that *Petromus* feeds to a significant degree on insects (WITHERS, 1979; apparently not known by GEORGE loc. cit.). Today a variety of food is reported to be taken (RATHBUN & RATHBUN, this volume) and

(*) Both authors equally contributed to this study.

rumination (including regurgitation and remastigation) would demand an elaborate gastro-intestinal apparatus, i.e. at least a proventriculus. The feeding capabilities of *Petromus* are still enigmatic. More information on these aspects, affecting the biology as well as the ecological significance of this species, is required. In the last couple of years, a breeding group of *Petromus* has been established and maintained successfully. Research so far deals with placentation and their evolutionary history (e.g., MESS, 1999b, 2001, 2003), external morphology (ADE, 1998, 1999; ADE et al., 2001) and general biology (e.g., MESS, 2002, 2005; MESS et al., 2000, 2002). Here, qualitative observations derived from the animals in captivity will be presented with special reference to nutrition, feeding behaviour and morphology of the digestive system. We will review scattered information about this poorly known species. Morphological data will help to integrate these data to a functional picture in the sense of "whole organism biology" (NOVACEK, 1998).

Fig. 1. – Habits, environment and feeding conductance of *Petromus* from a breeding colony.
A : *Petromus* 43, a male individual that was given to the Tierpark Berlin.
B : Interior of the animal house at the Humboldt-University of Berlin.
C : *Petromus* 4, a male individual feeding on his daily food from the feeding dish.
D : *Petromus* 27, a female engaged with reingestation of faecal droppings.

MATERIAL AND METHODS

The breeding group, started in 1995, is based on 8 animals from the RSA. The group is now housed at the Humboldt-University, Berlin, and was formerly bred at the Universities of Tübingen and Göttingen. Currently, the animals are housed in primate cages : 1 x 0.7 x 0.8m for single individuals or pairs, and double this space for family groups (Fig. 1b). Inside, several resting places and a nest box are offered, as well as the possibility for sand bathing. The animal house is characterised by the following parameters : about 25°C air temperature, 50% humidity, 12 hour light with additional daylight spots provided 4 to 6 hours each day (Fig. 1b).

The animals are fed with hay, i.e. hard-pressed pellets containing dried graminoids with about 26% raw fibre material (Sniff ® Heucobs). Moreover, once a day standard food pellets for chinchillas (Sniff ® Chi, based on plant fibres with 14% raw fibre content) or a mixed food for guinea pigs (Sniff ® Ms Müsli) is given. These dry foods contain a considerable amount of vitamin C. This industrially produced food is supplemented by a mixture of fresh plant material. Most frequently used are carrots (roots as well as green parts), tomatoes, paprika, cucumbers, radishes, kohlrabi, broccoli, maize, and more rarely apples, pears, grapes and other fruits are given. (Fig. 1c)Occasionally dried bread, sunflower seeds or nuts are given in addition. Finally, mineral supply is provided by small pieces of standard pet limestone and salt stones.

This study is based on qualitative observations on various animals from the breeding group. Occasionally, a time lapse video camera using infrared spectrum was used to observe the behaviour during the dark phase. Behaviour in captivity is compared with data derived

from field studies. The dassie-rats were conditioned to accept close observations by rewarding them with food and allogrooming by humans when approaching the animal keeper or student. This way it was possible to explore the direction of chewing movements by touching the working jaws.

Anatomical examination was conducted by gross morphological analysis using 60 fold magnification of the gastrointestinal tract of one female individual (*Petromus* Nr. 19 of the breeding colony) as well as of the morphology of the teeth and head region by using skulls and material from the wet collection that has been built up during the years. In particular, tooth structure is described on the basis of animals that have been born in the wild (*Petromus* SZ 7499, Zoologische Sammlung, University of Tübingen) as well as in captivity (*Petromus* Nr. 61 of the colony).

RESULTS

DESCRIPTION OF FEATURES ASSOCIATED WITH NUTRITIONAL BIOLOGY

1. Morphology of the digestive system and associated structures

Oral head region

The oral cavity, as in all rodents, is bipartite. A gnawing compartment and a chewing compartment are present. The compartments are produced by inwardly projecting "lips" (inflexa pellita) provided with micro vibrissae, separating the front or gnawing teeth, respectively, from the cheek teeth (Fig. 2a). These oral rim projections meet nearly at the median plane, separated by a well developed, longitudinally extending papilla palatina. The gnawing teeth are easily exposed by an upper lip cleft (Fig. 2a). The rhinarium of *Petromus* is strongly reduced; not even small narial pads are present (Fig. 2b). Instead, there are only small, reduced, inconspicuous cushions at the entrance of the nares (Fig. 2b). The chewing compartment proximal of the diastema ("filled" with the inflexa) consists of 4 cheek teeth (dP4, M1-3). The teeth possess deep transverse infolding of the enamel, referred to as bilophodont condition with an anterior protoloph and a posterior metaloph (sensu THENIUS, 1989, see Fig. 2c.) The borders of the lophs below (buccal side) and above (lingual side) form distinct cusps (Fig. 2c). As judged from the occlusion pattern, the grinding and shearing actions are not produced in the horizontal plane as in mainly grass-consuming hystricognaths (THENIUS, 1989). Instead, there is a more strongly developed vertical tooth relief. The relief indicates a "mortar- and- pestle" action (see LUCAS, 1979) as in dilambdodont teeth (e.g. *Tupaia*, THENIUS, 1989). This means that there is a marked transverse component of action during chewing. Reflecting this transverse component, the upper tooth row is markedly abraised at the buccal side (Fig. 2c), whereas, correspondingly, the lower interacting gnawing teeth show abrasion on the lingual side. The morphology of the jaw joint indicates that propalineal (back- and forth) movements are likewise possible, as in all rodents (see BUTLER, 1985; THENIUS, 1989).

The gastro-intestinal tract

The stomach is large. Moreover it is markedly curved, almost U-shaped (Fig. 2d). It has no transversely-running folds or septa producing proventriculus-like structures without glands as, e.g. in murids (Fig. 2d). There is a continuous layer of glands present as judged from gross morphological analysis. The caecum is large in diameter and strongly subdivided or haustrated (Fig. 2e). The transition area from the caecum towards the colon is inflated (Fig. 2e). The proximal part of the colon is moderately large in diameter. Dissection of the proximal colon region reveals that longitudinally-running ridges are present (Fig. 2f). Two prominent ridges run distally. Proximally, they are associated with some low oblique ridges in the transition zone between the caecum and the colon. The longitudinal ridges possess a transversely ridged surface structure. The two main ridges are closely apposed to each other, enclosing a distinct groove (Fig. 2f).

2. Behaviour associated with feeding

Feeding

The hands are used to hold the food during gnawing action (Fig. 1c). This is a remarkable process by which *Petromus* adjusts the position of the food item to the gnawing tooth (Fig, 1c; see also LANDRY, 1970). The food pieces lay between a groove formed by the reduced thumbs and the proximal and distal pads (for terminology of hand morphology see ADE & ZIEKUR, 1999). It appears that *Petromus* eats repeatedly during the whole day, especially on hay which is provided without restriction. In between feeding activities, extended resting phases take place, using the warm day-light spots. The animals are active every few hours during the night or dark phase, which is usually linked with feeding on hay or other available food. Both during day and night, the hay pellets are eaten either at the place where they have been deposited by the animal keepers or they are transported to where the dassie-rats prefer to sit down and rest. Fresh food and food pellets are more often eaten directly from the feeding dishes without transporting them (Fig. 1c). Within pairs or family groups, a female has first access to the feeding dish, especially when she is pregnant or lactating. Typically, conflicts at the feeding dish are settled by vocal dispute between the individuals and not by physical attacks. If such attacks occur they are usually not violent (our animals have been carefully accustomed to each other before putting them together).

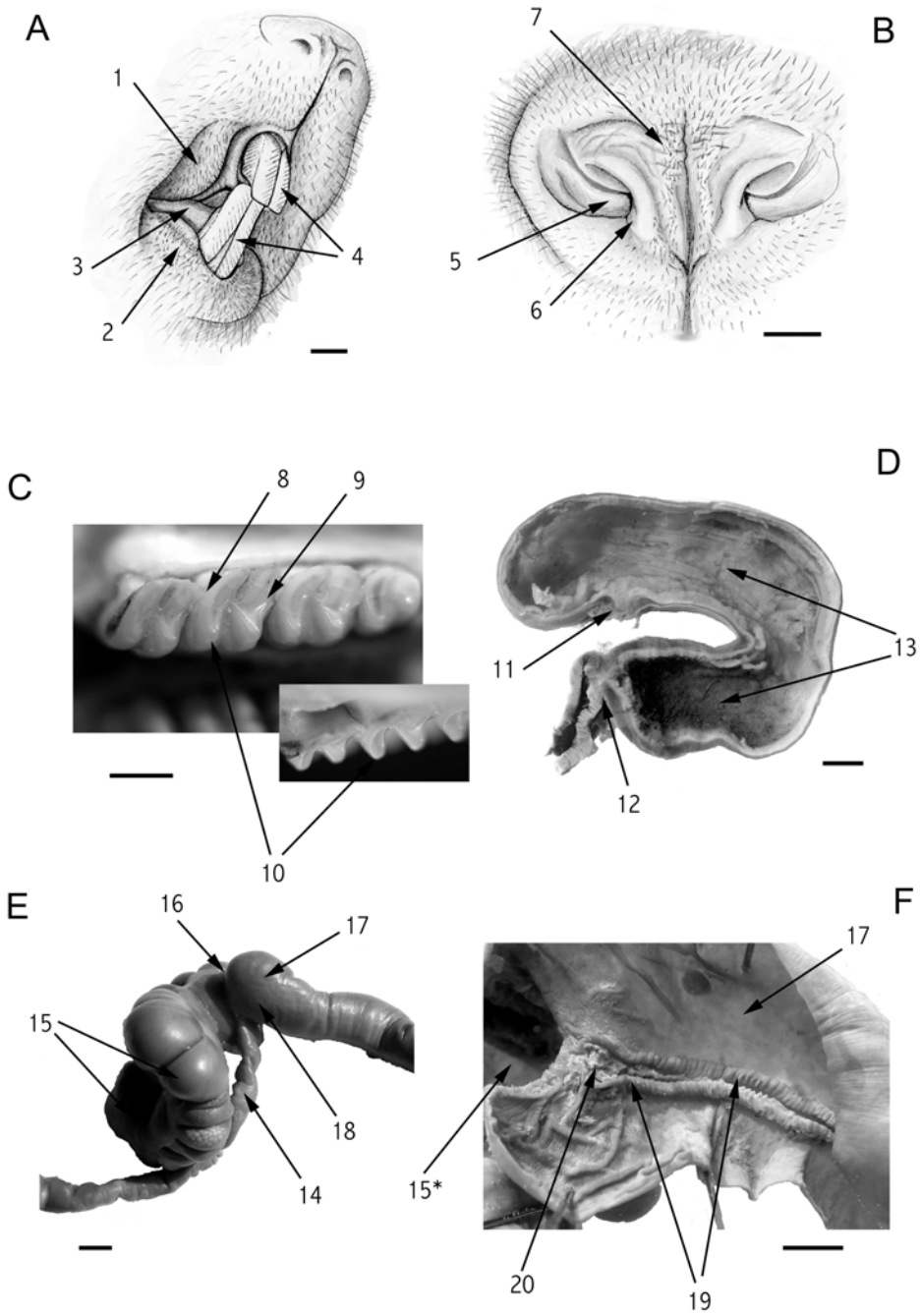

Fig. 2. – Morphology of oral head and gastro-intestinal tract in *Petromus typicus*.
A : The mouth cavity and gnawing teeth. Scale bar = 0.2 cm. (ADE, 1998).
B : The rhinaric region in a subadult individual. Scale bar = 0.1 cm. (ADE, 1998).
C : The left upper cheek teeth row (dP4, M1-3) of *Petromus* SZ 7499 from above (full-size photo) and from the buccal side (inlet) to demonstrate the distinct cusps. Accordingly, mesial is on the left hand side and buccal on top. Scale bar = 0.2 cm.
D : The stomach of *Petromus* 19 after macroscopic preparation. Scale bar = 0.5 cm.
E : Transition from the haustrated caecum into the proximal colon. Scale bar = 0.5 cm.
F : The proximal colon after preparation with longitudinal folds. Scale bar = 0.5 cm.

Abbreviations in Fig. 2 :

1 : upper inflexa pellita
2 : lower inflexa pellita
3 : the tongue
4 : upper and lower gnawing teeth (dI2)
5 : external opening of the nares
6 : inconspicuous rudiments of narial pads
7 : hairy parts in the rhinaric region
8 : protoloph of M1
9 : metaloph of M1
10 : cusp of M1, present at the lingual side
11 : opening of the oesophagus into the stomach
12 : pylorus, i.e. transition from stomach into proximal gut
13 : internal region of the stomach
14 : duodenum
15/15* : the caecum : external view and lumen of caecum
16 : transition zone between caecum and colon
17 : the proximal colon
18 : area of the colon possessing longitudinal folds inside
19 : longitudinal ridges inside the proximal colon
20 : groove between the ridges

Coprophagy

The animals are able to produce two different kinds of faecal droppings, dark brown ones which are considerably dry and a second type that is more greenish in colour and wet. It was never observed that a specimen consumes the brown pellets, but the greener ones were eaten frequently (Fig. 1d). It appears that a transitional production from brown to greenish faecal pellets occur. The two different sorts of pellets are easily recognised by the animals : When the droppings are changing their colour towards greenish, *Petromus* pick them up with the mouth and bite into it. If they are not appropriate – usually when the colour is still brownish – the droppings are immediately thrown away, and the next droppings that appear at the anus are tested again. Pellets of distinctly greenish colour are eaten, often chewing them a while before swallowing. The activity related to reingestation mostly occurs during the extensive resting periods.

Rumination, ”jack knife behaviour” and ”tail stand”

Although hundreds of hours have been spent observing different individuals of *Petromus*, it was not possible to find any indication for the occurrence of rumination as suggested in literature. Neither after the animals had eaten their daily amount of vegetables and food pellets, nor after feeding on hay at other times has an indication of rumination been found (Our *Petromus* have been accommodated to close sight contact by the observer). Rumination-related ”jack-knife behaviour” as described by COETZEE (1983), i.e. bending down of the head toward the abdomen, seems to be restricted to male individuals, and associated with the cleaning of the genitals. During the bending down action the penis is elongated to about double its normal length. Afterwards the penis is taken into the mouth and cleaned by moving the mouth up and down. Finally, after interrupting the close contact between mouth and penis, the individual jerks up upright, often chewing or smacking with its lip region. Such cleaning activities in males occur frequently, distributed throughout the day, indicating that the jack-knife action is a comforting behaviour. The newly described ”tail stand behavioural pattern”, which means that an animal stand on its front feet while propping up the hind feet and drumming them against the abdomen for several seconds has been suspected to be important for digestive efficiency (see Fig. 3 in RATHBUN & RATHBUN, this volume). This behaviour has been observed from time to time in captive animals from the breeding group too. It is more rare than, for instance, coprophagy or the jack-knife movements.

Food preferences

Petromus has been frequently observed to drink water, using the outlets of the water bottles. The tongue is used during water uptake. Hay is given ad lib. and the animals feed on the pellets repeatedly during the day. Standard pet limestones as well as salt stones are used sporadically. According to the consumption of fresh plant material, *Petromus* accepts a variety of various vegetables and fruits (see Material & Methods). It appears that *Petromus* have individual preferences with regard to the food offered. When extra food is given, it appears that the animals show a clear preference for seeds and nuts, but do not feed exclusively on them. Instead they switched between the extra food and hay pellets. Thus far, *Petromus* has never been observed to eat insects or other animals offered. Feeding trials have been conducted by using meal-worms or crickets. Even during pregnancy or lactation, the animals refused such food. Moreover, trials to feed them with pellets for hamsters and mice were not successful. Cheese or small amounts of meat products were not accepted.

DISCUSSION AND CONCLUSION

Petromus possesses characteristics of the naso-labial and oral region linked with a flexible diet. The bipartite organisation of the oral mouth cavity allows the gnawing teeth to be easily exposed and used for exploration, e.g. of food consistency or texture (ADE, 1998; LUCAS, 1979), while the inner part of the mouth is protected. In terms of evolution, the exploratively used gnawing teeth have replaced functions of the rhinarium, i.e. the originally tactile region of the head in rodents (ADE, 1998). According to the almost complete reduction of the rhinarium in *Petromus* and the fact that the animal projects the dorsum nasi rostrally and not the rhinaric region when exploring its surroundings, it can be concluded that the rhinaric region is not extensively used for specific exploration of the environment as i.e. in insectivorous terrestrial mammals. This is supported by behavioural observations comparing *Rattus norvegicus*, *Petromus typicus*, *Cavia porcellus and Octodon degus* (see observations of MESS & ADE described in ADE, 1998). Thus, extensive rummaging in the soil for insects is very unlikely. However, morphology does not preclude consumption of non-soil insects, i.e. insects from higher strata of the vegetation or surface running forms. *Petromus* has not been observed to feed on insects when we offered them to our captive animals. On the basis of observations on feeding behaviour, COETZEE (1983) came to the conclusion that *Petromus* is mainly herbivorous in the field. DE GRAAFF (1981), referring also to stomach contents, classifies the species as strictly feeding on plant matter (leaves, berries, seeds, flowers of compitae). GEORGE (1981) and COETZEE (1983) claim a preference for grasses. RATHBUN & RATHBUN (this volume) did not observe dassie-rats searching for, or eating, invertebrates. However, WITHERS (1979) has found a significant contribution of insects in stomach contents. The latter reference has not been cited in any paper except for RATHBUN & RATHBUN (loc. cit.).

The puncture-crushing mode with high and sharp cusps of the teeth, enabling similar sized mammals to use invertebrates as food (LUCAS, 1979; PFRETSCHMER, 1997), is not present in *Petromus*. The cusps of the cheek teeth of *Petromus* are blunt. During the mortar- and- pestle action, compressive forces should prevail. Referring to LUCAS (1979), our tentative conclusion is that the cheek teeth are more adapted to fracture plant material than invertebrate material. However, it cannot be excluded that the *gnawing teeth* may serve to puncture and crush exoskeletons, especially when bearing in mind the sophisticated ability to use the hands during the gnawing process. The cheek teeth may then also serve as crushing devices. In fact, crushing is the presumed major function of these kind of

teeth with blunt cusps (see THENIUS, 1989). Constraints on the amount of microfaunivory may come from the need to preserve a sufficiently dense population of cellulose processing micro-organisms in the intestinal tract (see below), i.e. a sufficient amount of cellulose has to be ingested to enable the animal to live solely from plant matter. This may be crucial when facing the dryness of the habitat, which is negatively correlated to the amount of invertebrates (SCHULTZ, 2000). Thus, we suspect that physiological regulation might suppress the consumption of invertebrates. Even WITHERS (1979) points out that *Petromus* is predominantly herbivorous, despite the fact that he notes a high proportion of insects in the stomachs of some specimens. The point is that it uses cellulose rich material.

The occlusion pattern of the cheek teeth, resembling omnivorous types of teeth (see THENIUS, 1989), indicates a less specialised mode of chewing compared to other Hystricognathi. This fits into the picture that *Petromus* utilises a variety of (plant) material ranging from stems, leaves to fruits and even insects. Strict herbivory, e.g. using high fibrous plant material is related to enamel ridges working in a more or less common horizontal grinding plane (BUTLER, 1985; PFRETSCHMER 1997). This is not the case in *Petromus*. Moreover, the cheek teeth are hypsodont but not continuously-growing, i.e. protection of the teeth from rapid abrasion by silicate containing material such as grasses is not well developed.

The stomach is large and curved, but internally undivided. This uniform cavity indicates that the stomach content will be exposed to an acid and enzymatic milieu. This implies two important consequences. 1) The milieu for the stomach content has a low pH preventing the effective establishment of micro-organism populations that could serve as fermenters and protein donors (proventriculus-function possibly in rodents (STARCK, 1995) and ruminants). 2) The chymus is itself acidic and contains enzymes. Both could strongly affect the mucosa. This means that rumination would be detrimental if there is no extensive buffering by mucus in the oesophagus and oral cavity. The latter is unlikely, and completely unknown, for mammals. Furthermore, the data derived from the laboratory group suggest that the so-called "jack-knife behaviour" described by COETZEE (1983) can not be confirmed to be associated with rumination. A similar behaviour occurs restricted to male individuals when cleaning the penis. The animals regularly show chewing movements afterwards without any indication of food matter inside the mouth. Thus, it appears likely that this behaviour belongs to comfort behaviour (including masturbation which might explain the chewing and smacking afterwards, G. RATHBUN, pers. comm.). The ingested plant material is most likely fermented by micro-organisms in the intestinal tract. The caecum is large and haustrated in comparison to hystricognaths with marked herbivorous and high fibrous diet, such as the chinchilla (TULLBERG, 1899/1900). Large caecae are typical for herbivorous rodents (HESSE & DOFLEIN, 1935; WITHERS, 1979). Longitudinal folds in the proximal colon reveal that a colon separating mechanism (CSM) as the structural prerequisite of coprophagy is present. This is supported by the production of special feacal droppings and their ingestion (also WITHERS, 1979). The CSM creates a selected reflux of chymus into the caecum as the basis for the production of specialised pellets which contain a significantly higher amount of vitamins and protein (BJÖRNHAG & SNIPES, 1999; HOLTMAIER, 2002). Thus, the ability to use high fibre matter for energy and protein production has to be assumed for *Petromus*. The fact that captive specimens consume high fibrous graminoid material all day long, even if energetically more rewarding food is available suggests that there is conspicuous dependency on this kind of food.

The newly described "tail-stand behaviour" (RATHBUN & RATHBUN, this volume) is seen from time to time in the caged animals. It is suspected by RATHBUN & RATHBUN that this behaviour is related to digestive efficiency by mechanical stimulation and support of peristaltic movements of the intestine.

Judged from the data on morphology and behaviour, *Petromus* is 1) a hindgut fermenter of cellulose with a special mechanism to utilise micro-organisms as a source of protein and vitamin supply, 2) depending mainly on plant matter, but the variety of food in this regard is large, 3) not confined to high fibrous plant material, but able to use this kind of material successfully in various combinations, and 4) not micro-faunivorous to a large degree. The CSM enables the animals to produce foreign protein within themselves which hints that they are potentially independent from animal protein. In summary, a great variety of food is used. This hints at the ability of *Petromus* to cope with unstable environments as is the case in xeric areas, such as in the Southern African Subregion.

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LITERATURE CITED

ADE, M. (1998). *Zur Evolution des Rhinariums der Glires. Eine Rekonstruktion auf phylogenetisch-systematischer Grundlage*. Wissenschaft & Technik Verlag, Berlin.

ADE, M. (1999). Macroscopic study on the rhinarium of the Lagomorpha. With special reference to the glires hypothesis. *Mitteilungen aus dem Museum für Naturkunde zu Berlin, Zoologische Reihe*, 75 : 191-216.

ADE, M., S. FRAHNERT & A. MESS (2001). Die Rekonstruktion der Evolution des Nahrungserwerbsapperates der Glires (Rodentia + Lagomorpha) als Beitrag für die Analyse ökologischer Fähigkeiten der Rodentia. *Mammalian Biology*, Sonderheft Bd., 66 : 6-7.

ADE, M. & I. ZIEKUR (1999). The forepaws of the rodents *Cryptomys hottentotus* (Bathyergidae) and *Nannospalax ehren-*

bergi (Muridae, Spalacinae) : Phylogenetic and functional aspects. *Mitteilungen aus dem Museum für Naturkunde zu Berlin, Zoologische Reihe*, 75 : 11-17.

BJÖRNHAG, G. & R.L. SNIPES (1999). Colonic separation mechanism in lagomorph and rodent species. *Mitteilungen aus dem Museum für Naturkunde zu Berlin, Zoologische Reihe*, 75 : 275-281.

BUTLER, P.M. (1985). Homologies of molar cusps and crests, and their bearing on assessments of Rodent phylogeny. In : LUCKETT & HARTENBERGER (eds), *Evolutionary relationships among rodents. A multidisciplinary analysis*. Nato ASI Series A, Vol. 92, Plenum Press, New York : 381-401.

COETZEE, C.G. (1983). The feeding behaviour of *Petromus typicus* A. Smith, 1831 (Rodentia : Petromuridae). *Annals Musee Royal De L'Afrique Centrale Tervuren – Belgique, Sciences Zoologiques*, 237 : 203-206.

COETZEE, C.G. (2002). The distribution and breeding season of the dassie-rat, *Petromus typicus* (Petromuridae, Rodentia). *Folia Zoologica*, 51 Suppl. 1 : 23-35.

ELLERMAN, J.R. (1940). *The families and genera of living rodents. Volume I. Rodents other than Muridae*. Trustee of he British Museum of Natural History, London.

GEORGE, W. (1981). The diet of *Petromus typicus* (Petromuridae, Rodentia) in the Augrabies Falls National Park. *Koedoe*, 24 : 159-167.

GEORGE, W. & G. CROWTHER (1981). Space partitioning between two small mammals in a rocky desert. *Biological Journal of the Linnean Society*, 15 : 195-200.

GRAAFF, G. DE (1981). *The rodents of Southern Africa*. Butterworths, Durban & Pretoria.

HESSE, R. & F. DOFLEIN (1935). *Tierbau und Tierleben in ihrem Zusammenhang betrachtet. Erster Band : Der Tierkörper als selbständiger Organismus*. Fischer, Jena.

HOLTMEIER, F.-K. (2002). *Tiere in der Landschaft. Einfluss und ökologische Bedeutung*. Ulmer, Stuttgart.

LANDRY, S.O. Jr. (1970). The Rodentia as omnivores. *Quarterly Review of Biology*, 45 : 351-372.

LUCAS, P.W. (1979). The dental-dietary adaptations of mammals. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 8 : 486-512.

MCKENNA, M.C. & S.K. BELL (1997). *Classification of mammals above the species level*. Columbia University Press, New York.

MEESTER, J. (1965). The origins of the southern African mammal fauna. *Zoologica Africana*, 1 : 87-95.

MESS, A. (1999a). The rostral nasal skeleton of hystricognath rodents : evidence on their phylogenetic interrelationships. *Mitteilungen aus dem Museum für Naturkunde zu Berlin, Zoologische Reihe*, 75 : 19-35.

MESS, A. (1999b). Plazentation von *Petromus typicus*, ein Beitrag zur Reproduktionsbiologie und evolutiven Differenzierung der Hystricognathi. *Courier Senckenberg*, 215 : 153-157.

MESS, A. (2001). Evolutionary differentiation of placental organisation in hystricognath rodents. In : DENYS, GRANJON & POULET (eds), *African Small Mammals*, IRD Éditions, collection Colloques et séminaires. Paris : 279-292.

MESS, A. (2002). *Petromus typicus* : reproductive biology of a poorly known animal. *Research Commitee Newsletter*, 8 : 38-40.

MESS, A. (2003). Evolutionary transformations of chorioallantoic placental characters in Rodentia with special reference to hystricognath species. *Journal of Experimental Zoology*, 299A : 78-98.

MESS, A. (2005) : Felsenratte. In : GRANSLOßER, U. (ed.), *Die Sozialsysteme der Säugetiere*. Filander Verlag, Fürth : 156-158.

MESS, A., T.B. HILDEBRANDT, M. FAßBENDER, R. HERMES & F. GÖRITZ (2000). Placentation and embryonic development of *Petromus typicus* (Rodentia, Hystricognathi, Petromuridae) : results on ultrasonic examination and selected morphological data. *Advances in Ethology*, 35 : 98.

MESS, A., B. MOHR & T. MARTIN (2001). Transformations in the stem species pattern of hystricognath Rodentia and the climatic change in the Eocene to Late Oligocene time interval. *Mitteilungen aus dem Museum für Naturkunde zu Berlin, Zoologische Reihe*, 77 : 193-206.

MESS, A., J. PINT & K. FAUST (2002). Ontogenetic differentiation in *Petromus typicus* : a basis for more detailed interpretation of results on ultrasonic approaches in a precocial rodent. *Advances in Ethology*, 37 : 145.

NOVACEK, M.J. (1998). In : BUTLER, D. Museums research comes off list of endangered species. *Nature*, 394 : 115-117.

NOWAK, R.M. (1999). *Walker's Mammals of the World*. Johns Hopkins University Press, Baltimore.

PFRETSCHMER, H.-U. (1997). Biomechanik des Zahnschmelzes. In : ALT & TÜRP (eds), *Die Evolution der Zähne. Phylogenie – Ontogenie – Variation*, Quintessenz Verlag, Berlin : 391-400.

RATHBUN, G.B. & C.D. RATHBUN (this volume). Dassie-rat (*Petromus typicus*) feeding ecology and petrophily. *Belgian Journal of Zoology.*

SCHULTZ, J. (2000). *Handbuch der Ökozonen* (S. 364-403 : Tropische/Subtropische Trockengebiete). Eugen Ulmer, Stuttgart.

SKINNER, J.D. & R.H.N. SMITHERS (1990). *The mammals of the Southern African subregion*. University of Pretoria, Pretoria, RSA.

STARCK, D. (1995). Teil 5 : Säugetiere. In : STARCK (ed), *Bd. 2. Wirbeltiere. Lehrbuch der Speziellen Zoologie* (begr. v. KAESTNER, A.), Fischer, Jena, Stuttgart, New York : 1-1241.

THENIUS, E. (1989). Zähne und Gebiß der Säugetiere. In : NIETHAMMER, SCHLIEMANN & STARCK (eds), *Handbuch der Zoology, Volume VIII Mammalia*, de Gruyter, Berlin.

TULLBERG, T. (1899/1900). *Ueber das System der Nagethiere : eine phylogenetische Studie*. Akademische Buchdruckerei, Uppsala.

VAUGHAN, T.A., J.M. RYAN & N.J. CZAPLEWSKI (2000). *Mammalogy.* Sanders College Publ., Fort Worth.

WILSON, D.E. & D.M. REEDER (1993). *Mammal species of the world. A taxonomic and geographic reference*. Smithsonian Institution Press, Washington, London.

WITHERS, P.C. (1979). Ecology of small mammal community and a rocky outcrop in the Namib desert. *Madoqua*, 2 : 229-246.

WITHERS, P.C. (1983). Seasonal reproduction by small mammals of the Namib desert. *Mammalia*, 47, 105-204.

WITHERS, P.C., G.N. LOUW & J. HENSCHEL (1980). Energetics and water relations of Namib desert rodents. *South African Journal of Zoology*, 15 : 131-137.

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Reproductive rhythm of the grass rat, *Arvicanthis abyssinicus*, at the Entoto Mountain, Ethiopia

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ABSTRACT. Data on the reproductive rhythm of the grass rat, *Arvicanthis abyssinicus*, were collected in a bush area and a crop field at the Entoto Mountain for a one-year period from August 2000 to July 2001. Very few individuals of *Arvicanthis* were captured from the bush area. The number of captures from the crop field, however, was much higher. Higher percentages of reproductively active males and females were recorded during the rains and the couple of months that followed. Breeding decreased in the dry months. The presence of cereals on the field did not seem to augment breeding during the dry months. The outcome of the present study is consistent with most previous results where breeding in *Arvicanthis* sp. primarily occurs during the rains and the few months that follow. It is recommended that physiological studies should be conducted for a better understanding of the reproductive timing of *Arvicanthis* in an eco-physiological context.

KEY WORDS : Entoto, Breeding rhythm, *Arvicanthis abyssinicus*, Ethiopia.

INTRODUCTION

Arvicanthis (Lesson, 1822) is an endemic genus to Africa and distributed along the equatorial belt from Senegal to Somalia and across the Nile Delta from Egypt to Tanzania (DELANY & MONRO, 1986). It is identified as one of the major pest rodents whenever occurring around cultivated lands (TAYLOR & GREEN, 1976). The taxonomy of the genus is controversial. With an understanding of the need for further revision of its taxonomy, populations of the Nile Delta and West Africa are conventionally grouped under *Arvicanthis niloticus* (Ruppell, 1842). About 5 species are described from East African populations. These are *A. blicki* (Frick, 1914), *A. abyssinicus, A. dembeensis* (Ruppell, 1842), *A. somalicus* (Thomas, 1903) and *A. lacernatus.* The first 4 species occur in Ethiopia (YALDEN et al., 1976). Some authorities tend to lump *A. dembeensis* with *A. abyssinicus* (MUSSER & CARLETON, 1993).

The breeding rhythm of the genus is well documented in various parts of Africa. However, results show that further investigations are always needed to understand its breeding rhythm more comprehensively. Most studies show that breeding in *Arvicanthis* begins with the start of the rains (DELANY, 1964; GHOBRIEL & HODIEB, 1982; FISHER, 1991; BEKELE & LEIRS, 1997). Even then, the exact timing of breeding during the rainy season showed inconsistencies. In Central Kenya, *Arvicanthis* started breeding few weeks after the start of the rains (NEAL, 1981). While in Nakuru, another Kenyan locality, breeding began about a month later (DELANY & MONRO, 1986). In Nigeria, breeding began a month before the rains (RABIU & FISHER, 1989). In Ethiopia and Burkina Faso, however, *Arvicanthis* bred only during the dry season (MULLER, 1977; SICARD et al., 1996). NEAL (1981) reported a year round reproduction in Western Uganda where the climate is described as uniform and less seasonal.

Several explanations have been proposed to explain the various patterns of reproductive timing in *Arvicanthis*. SICARD et al. (1996) suggested that *Arvicanthis* stopped breeding during the rainy season in Burkina Faso due to the gonadoinhibitory effect of long day photoperiod that prevails during the season. MULLER (1977), on the other hand, explains his observation on Ethiopian *Arvicanthis* as one happening due to physiological stress from the cold in the Simien Mountain Highlands of the country. He suggested that the rats could be physiologically too stressed to reproduce under the prevailing cold. NEAL (1981) did not observe any correlation between quality of food and reproduction in central Kenya. Rather, he attributes the cessation of breeding at the end of the dry season to increased temperature. He also concludes, based on his results from Western Uganda, that *Arvicanthis* is capable of continuous breeding and as such the question that shall be addressed is "What makes *Arvicanthis* to stop breeding?" and not "What initiates it to?" GHOBRIEL & HODIEB (1982) on the contrary, emphasized the importance of nutritious food (cereals, seeds and animal matter) in playing crucial role to determine the timing of breeding in *Arvicanthis*. The gonadostimulatory effect of green stuffs and the availability of drinking water were also suggested by other researchers (References in NEAL, 1981) to explain the reproductive timing of *Arvicanthis.*

The present study documents data on the breeding activity of *A. abyssinicus* at the Entoto Mountain, Ethiopia from August 2000 to July 2001.

METHODS

The Entoto Mountain is located about 8 km North of Addis Ababa. Most part of the mountain is covered with eucalyptus trees. The forest is under government protection. Part of it is inhabited by farmers who cultivate cereal crops like wheat, barley, and teff. Since eucalyptus trees discourage growth of ground cover, rodents were not expected to be found in the forest proper of the mountain. Within the forest there were clearings covered with dense bushes which were thought more suitable for rodents. One area (100 m x 50 m) with this kind of vegetation (height up to 175 cm) was selected to be one of the two study sites. It was dominated by plant species like *Helichrysum shimperi, Chilocephalum shimperi, Echinops macrochaetus* and *Conyza schimperi*. The grass species *Andropogon amethystinus* was also found abundantly. The second study site was established inside and around a cultivated land. This site was planted with barley. The two sites were distantly separated (about 4 km) with few chances of migration of rodents between one another.

The study area has one rainfall peak during the months of June-August. During the study period, there was also a small rainy period in March and May. The smallest amount of rainfall was recorded during the months October to February. February was the month with the highest average maximum temperature while December and January recorded the lowest (Fig. 1a).

In the bush, trapping started at the beginning of August and continued for a year on a monthly interval. In the crop field trapping started from November. Each trapping session of the month lasted for three consecutive days and nights. Victor Mouse Snap Traps were used (small and large versions). Traps baited with peanut butter were set near rodent pathways, burrows or sites with good bush cover under rocks and in crevices. Traps were checked in the morning (9 :00 a.m.) and late afternoon (5 :00 p.m.). After retrieving the catches, standard body measurements (body weight and length of head-body, tail, hind foot and ear) were taken. Females with perforate vagina, large nipples or well vascularized and distended uteri were considered to be reproductively active. If implanted embryos were observed, they were identified as pregnant. Males with scrotal testes, very well visible epididymal tubules and large seminal vesicles were considered to be sexually active. Individuals that weighed less than 35 g were identified as juveniles, since there were no individuals below that weight, which showed any sign of sexual maturity.

TABLE 1

Captured rodents from the two study sites at Entoto Mountain.

Species	Bush	Crop
Arvicanthis abyssinicus	24	167
Desmomys harringtoni	126	7
Praomys albipes	74	32
Lophyromys flavopantatus	34	17
Total	**258**	**223**

RESULTS

A total of 481 rodents belonging to four species were captured (Table 1). Of these, 258 were captured in the bush habitat and the other 223 in the crop field. The bush habitat rodent fauna was dominated and heavily infested by *Desmomys harringtoni* (Thomas, 1903) with a total capture of 126 individuals (48.8%) while *Arvicanthis abyssinicus* was the least abundant (n=24) making up only 9.3% of the total. On the other hand, the crop field was completely dominated by *A. abyssinicus* (n=167 or 74.9 %) and *D. harringtoni* was the least abundant species (n=7 or 3.1%). The other two species, *Praomys albipes* (Ruppell, 1842) and *Lophyromys flavopunctatus* (Thomas, 1888), were also more abundant in the bush habitat than in the crop field (Table 1).

TABLE 2

Seasonal variation of captured *Arvicanthis abysinicus* from the bush habitat (light font) and the crop field (bold font)

	2000			2001								
	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.
Females	0	3	2	2	0	1	0	0	0	0	0	0
				3	**11**	**15**	**16**	**8**	**6**	**5**	**8**	**4**
Males	2	5	2	2	0	0	0	0	0	0	1	0
				4	**3**	**13**	**18**	**13**	**8**	**6**	**9**	**2**
Juveniles	0	0	0	0	1	3	0	0	0	0	0	0
				3	**2**	**3**	**2**	**3**	**1**	**0**	**0**	**1**
Total	2	8	4	4	1	4	0	0	0	0	1	0
				10	**16**	**31**	**36**	**24**	**15**	**11**	**17**	**7**

Table 2 summarizes the catch distribution of *A. abyssinicus* in both study sites. In the bush area, the highest number of *A. abyssinicus* was recorded in September while between February and July none was captured except for the single specimen in June. The adult male to female sex ratio was 1.4 :1. Only 4 juveniles were captured, in December and January. In the crop field, the highest numbers of *A. abyssinicus* were recorded in February (n=36), the lowest in July (n=7). The male to female sex ratio was 1 :1.

Figure 1B shows the percentage of reproductively active males and females from the crop field. Higher proportions of reproductively active males and females were obtained during the rains and the first two months that followed. In the crop field, there was a high percentage of reproductively active males and females in November

and December. During these two months, all the captured males were sexually active and except for one individual in December, all the females were pregnant. Reproductive activity declined in both sexes from January onwards. For the bush area, data were too scarce to discuss reproduction.

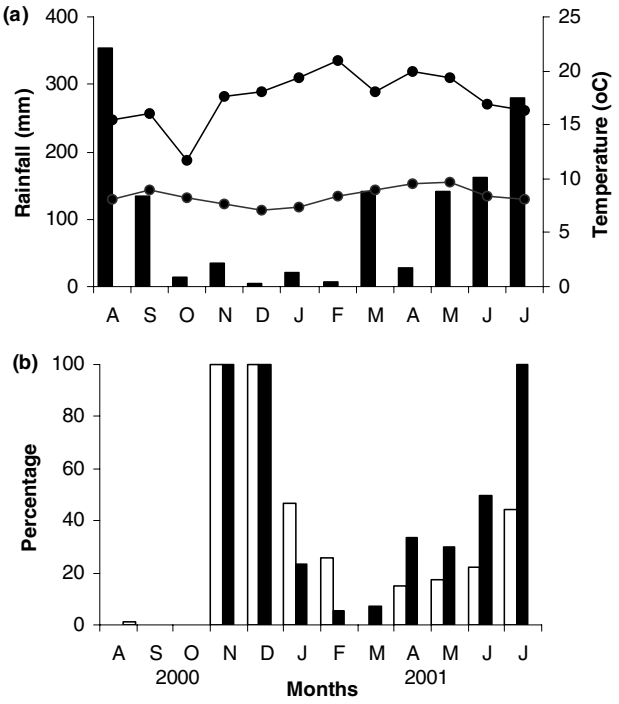

Fig. 1. – (a) Monthly total rainfall (bars) and average maximum and minimum temperature (lines) and (b) percentage of reproductively active males and females from the crop field (white bars : females;

DISCUSSION

A. abyssinicus was always rare or absent in the bush area. Earlier studies showed that *Arvicanthis* prefers habitats which have good hiding places and aerial cover (WUBE & BEKELE, 2001). The bush habitat of the present study was also such a habitat. However, it can be suggested that *Arvicanthis* here gave priority to cultivated fields where cereals can be obtained abundantly while avoiding the less nutritious and crowded bush area. During the study period, the bush habitat harboured a number of other rodent species while *A. abyssinicus* dominated the crop field. Generally it can be hypothesized that, 1) there might have been competition among rodents of the region for the most nutritious crop fields and the competition ended in favour of *A. abyssinicus* while the rest of the species were relegated to the bush habitat or 2) the other rodent species did not show interest for the crop habitat even though it was nutritious. Rather they gave priority to the presence of cover and hiding places while *A. abyssinicus* managed to survive in the more exposed crop fields by digging nests and taking refugee under the available rocks and crevices. It has been suggested earlier that there is always one dominant species in an area which is shared by different populations that have similar niche (FOX & BROWN, 1993).

In the crop habitat several individuals of *A. abyssinicus* were captured. The observed reproductive activity rhythm was in conformity with most previous observations that report peak reproduction in *A. abyssinicus* during and shortly after the rains (TAYLOR & GREEN, 1976; NEAL, 1981; GHOBRIEL & HODIEB, 1982). Of course, in the present study it is not clear what happened during August - October 2000 because the data collection started only in November. Even then, the fact that the reproductive activity started to increase together with the start of the rain in the 2001 rainy season i.e. June, it could be reasonable to speculate that there had been the same trend during August - October 2000.

Reproductive activity was highly reduced during the dry months, despite the presence of cereals (nutritious food) in that season. This was against Taylor and Green's observation in Western Uganda where artificially supplied cereals modified the breeding peak (TAYLOR & GREEN, 1976). Even though the barley harvest was completely collected in April and May, the crop was on field during all the previous months. If the presence of cereals had any gonadostimulatory influence, the percentage of reproductively active *A. abyssinicus* should not have significantly decreased in the dry months. However, this needs to be substantiated by data from a longer study period.

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REFERENCES

BEKELE, A. & H. LEIRS (1997). Population ecology of rodents of maize fields and grassland in central Ethiopia. *Belg. J. Zool.*, 127 : 39-48.

DELANY, M.J. (1964). A study of the ecology and breeding of small mammals in Uganda. *Proc. Zool. Soc. Lond.*, 142 : 347-370.

DELANY, M.J. & R.H. MONRO (1986). Population Dynamics of *Arvicanthis niloticus* (Rodentia Muridae) in Kenya. *J. Zool., Lond.*, 209 : 85-103.

FISHER, M. (1991). A reappraisal of the reproductive ecology of *Arvicanthis* in Africa. *Afr. J. Ecol.*, 29 : 17-27.

FOX, B.J. & J.H. BROWN (1993). Assembly rules for functional groups in north American desert communities. *Oikos*, 67 : 358-370.

GHOBRIEL, I. & A.S.K. HODIEB (1982). Seasonal variations in the breeding of the Nile rat (*Arvicanthis niloticus*). *Mammalia*, 46 : 320-333.

MULLER, J.P. (1977). Population okologie von *Arvicanthis abyssinicus* in der grassteppe des Semien Mountains National Park (Athopien). *Z.Saugetierk.*, 42 : 145-172.

MUSSER, G.G. & M.D. CARLETON (1993). Family Muridae. In : WILSON, D.E. & D.H. REEDER (eds), *Mammal species of the world. A taxonomic and geographic reference.* Washington D.C. : Smithsonian Press : 501-755.

NEAL, B.R. (1981). Reproductive biology of the unstriped grass rat, *Arvicanthis,* in East Africa. *Z. Saugetierk.*, 46 : 174-189.

RABIU, S. & M. FISHER (1989). The breeding season and diet of *Arvicanthis* in northern Nigeria. *J. Trop. Ecol.*, 5 : 375-386.

SICARD, B., D. MAUREL, F. FUMINIER & J. BOSSIN (1996). Climate, trophic factors and breeding patterns of the Nile grass rat (*Arvicanthis niloticus solatus*) : a 5 year study in Sahlian region of Burkina Faso (formerly Upper Volta*). Can. J. Zool.*, 72 : 201-214.

TAYLOR, K.D. & M.G. GREEN (1976). The influence of rainfall on diet and reproduction in African rodent species. *J.Zool.Lond.*, 180 : 367-389.

WUBE, T. & A. BEKELE (2001). Habitat preference of the African grass rat, *Arvicanthis dembeensis* (Rodentia, Muridae), in Koka, Central Ethiopia. In : DENYS, C., L. GRANJON & A. POULET (eds), Proceedings of the 8th African Small Mammals Symposium, Paris, France. 499-510.

YALDEN, D.W., M.J. LARGEN & D. KOCK (1976). Catalogue of the mammals of Ethiopia. 2. Insectivora and Rodentia. *Mon.Zool.Ital*. (N.S.) (Suppl.).

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Comparative physiology of heat production in rodents under increasing salinity : The effects of habits and habitat

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ABSTRACT. Small mammals inhabiting environments that are either seasonally or perpetually dry, such as Mediterranean or desert ecosystems respectively, commonly have physiological capabilities that enable them to deal with water shortage. We compared results of thermoregulatory responses of rodent species inhabiting different habitats and having varying activity periods, when salinity increases in their water source, as often occurs in their natural habitats during the dry period.

Experimental animals were maintained on a diet of dry soy-beans and an increased salinity of their water source (2% agar gel), from 0.9% to 3.5% NaCl in mesic species and up to 7% in xeric species. While desert species could cope with high salinities in their water source, mesic species could not. Desert-adapted species depending on their preferred micro-habitats differ in their thermoregulatory responses. Rock dwellers, such as the golden spiny mouse *Acomys russatus* and the bushy tailed gerbil *Sekeetamys calurus*, reduce their resting metabolic rates (RMR) and increase nonshivering thermogenesis (NST) capacity in response to increasing salinity. In contrast, the deep burrowing fat jird *Meriones crassus*, increases RMR and only slightly increases NST-capacity.

Our study suggests that species occupying different habitats vary their thermoregulatory capabilities, in relation to dehydration and increasing salinity in the water source. This may be a consequence of adaptation from the original ecosystem to the current environment in which a species inhabits.

KEY WORDS : Nonshivering thermogenesis, resting metabolic rate, aridity, thermoregulation, kidney function

INTRODUCTION

Small mammals must find their food and water resources in their immediate surroundings. Therefore, they can be used as indicators of habitat quality. Israel, being a transition zone for biogeographically different regions (TCHERNOV & YOM-TOV, 1988), inhabits rodent species of different evolutionary origins. Furthermore, the landscape changes in relation to precipitation and altitude, from a sub-alpine ecosystem on Mount Hermon, through the Mediterranean and steppe ecosystems and finally to the extreme arid ecosystem. Rodent species show different distribution patterns, ranging from the occupation of a single ecosystem as the golden spiny mouse *Acomys russatus* (arid ecosystem), through to species with wide distributional ranges as in the case of the common spiny mouse *A. cahirinus* (arid, steppe and Mediterranean ecosystems).

A comparison of physiological variables, such as water economy and heat production, between different species from disparate environments, or divergent populations within the same species from distinct habitats, is of significant importance for the understanding of adaptation to the environment. Studies (SCHMIDT-NILSEN, 1964; SHKOLNIK & BORUT, 1969; WEISSENBERG & SHKOLNIK, 1994) have demonstrated that efficient water economy can be examined through the ability of the kidney to produce a concentrated urine, and efficient heat economy is typified by resting metabolic rates (RMR) that are lower than the expected from body mass, according to allometric equations (KLEIBER, 1961; HART, 1971; HAIM & BORUT, 1981; HAIM, 1987; HAIM & IZHAKI, 1993). The relative medullary thickness (RMT) is an anatomical variable that can be used for predicting kidney function (SPERBER, 1944; SHKOLNIK, 1988; WEISSENBERG & SHKOLNIK, 1994). Therefore, it is expected that species with high RMT indices will be able to increase their urine concentration during spells of drought that lead to increased salinity of water sources.

Deserts can be cold at nights, and endotherms such as rodents that possess low RMR's have to increase heat production over a short period to maintain their body temperature (HAIM & LEVI, 1990). Nonshivering thermogenesis (NST) is an important mechanism for heat production in small mammals such as rodents (JANSKY, 1973). Furthermore, this mechanism has been found to compensate for the lower RMR values in species like desert rodents (HAIM & IZHAKI, 1993).

The objectives of this study were to compare the thermoregulatory responses of different rodent species subjected to osmolarity challenges. Specifically, to examine : (1) If such a challenge will have an impact on heat production, by means of NST? (2) If NST values can be related to the pattern of activity and habitat? This paper

compares five different species of rodents, some of an African origin, that occur in Israel, while others are of a Palearctic origin but occur also in Africa.

MATERIAL AND METHODS

Animals

Data were collected on the following rodents : Common spiny mouse (*Acomys cahirinus*), Golden spiny mouse (*Acomys russatus*), Bushy tailed gerbil (*Sekeetamys calurus*), Fat jird (*Meriones crassus*), Tristram's jird (*Meriones tristrami*) (Table 1). In all instances the experimental animals were fed crude soybeans that were dried for 48h at 60ºC to a constant weight. Water was supplied in the form of 2% agar gel (20g of dry agar dissolved in 1000ml of de-ionized water) to which desired salinity levels were achieved by dissolving appropriate amounts of NaCl. Body mass was measured every second day, during the acclimation periods. When a loss of more than 20% in body mass was recorded, the experimental individual was removed from the experiment. Following each acclimation period (14 days) to a given salt concentration, urine volume, urine osmolarity and nonshivering thermogenesis (NST) variables were measured.

TABLE 1

Characteristics of the studied species, data are taken from HARRISON & BATES (1991).

Species	Region	Habitat	Activity
A. russatus	Xeric	Rock dweller	Diurnal
A. cahirinus	Mesic	Rock dweller	Nocturnal
S. calurus	Xeric	Rock dweller,	Nocturnal
M. crassus	Xeric	Burrow	Nocturnal
M. tristrami	Mesic	Burrow	Nocturnal

Urine collection and variables analysis

For each level of salinity, the animal was placed in a mesh net cage (19.5 x 11.5 x 9cm) above a sheet of Parafilm for a period of 24h. Urine was collected with a Pasteur pipette and subsequently placed into Eppendorff tubes and stored at 4ºC every 6h. Urine volume was measured using a Gilson pipette to the accuracy of 1µl. Urine Osmolarity was measured using a Wescor 5500 Vapor Pressure Osmometer (PALGI & HAIM, 2003).

NST variables

Oxygen consumption (VO_2) was measured using an open flow system (DEPOCAS & HART, 1957). The air was pumped into the metabolic chamber using a pump (Aqua-Serene). Oxygen concentrations were measured from the air exiting the metabolic chamber using, an oxygen analyzer (Servomex 750A) connected to a multimitter (Tabor). The air was dried with a silica-gel column at the entrance and exit ports of the metabolic chamber.

Resting metabolic rate (RMR) was measured for each species as the minimal oxygen consumption (VO_2Min) at 1ºC below its lower critical temperature. Body temperature (T_b Min) was measured at the end of VO_2Min measurements, by inserting a copper-constantan thermocouple 3cm deep into the rectum of the experimental individual. The thermocouple was connected to a TH-65 Wescor digital thermometer.

VO_2NA was measured as the maximal response of VO_2 to a noradrenalin (NA) injection (Sigma) 1.5mg/Kg (HELDMAIER, 1972; HAIM et al., 1995). Approximately 20min. after VO_2NA values were achieved and VO_2 levels started to decline, the experimental individual was removed from the metabolic chamber and its body temperature was measured once again and presented as T_bNA. NST-capacity was calculated as the ratio of VO_2NA to VO_2 Min (RON & HAIM, 2001; SCANTLEBURY et al., 2002).

Statistics : All values are given as mean ± SD for n = 7. Results showed a normal distribution and therefore Student *t-test* was used for statistical analysis.

RESULTS

A marked difference was noted between species from mesic and xeric habitats. The xeric species comprising *S. calurus*, *A. russatus* and *M. crassus*, survived on agar with a 7% salinity, whereas the mesic species *M. tristrami* and *A. cahirinus* were only able to withstand 3.5% (Table 2). *Meriones crassus* showed the lowest drop of body mass (10.1%) when acclimated to 7% salinity (Table 2). The highest osmolarity values in urine were recorded in *A. russatus* and *M. crassus* (Table 3), and among the desert species the lowest values were found in *S. calurus*.

TABLE 2

The response of body mass to increased salinity in the water source of dehydrated individuals, of different studied rodent species. Values presented as total body mass (gr) for 0.9%; 3.5% (mesic species) and 7% (xeric species) salinity of the water source and as the % difference between salinities. Data for *A. russatus* is from RON & HAIM (2001); for *A. cahirinus* from SHANAS et al. (2003); for *S. calurus* from PALGI & HAIM (2003); for *M. Crassus*, from HAIM (UNPUBLISHED) and for *M. tristrami,* from NEUMAN et al. (2000).

Species	Salinity (%)	Wb (gr)		Wb (%)
A. russatus	0.9	50.4	±6	22.6
	7	39.0	±8.2	
A. cahirinus	0.9	43.1	±7	19.5
	3.5	34.7	±7.6	
S. calurus	0.9	59.7	±9.2	19.1
	7	48.9	±5.5	
M. crassus	0.9	100.1	±15.8	10.1
	7	90.0	±9.3	
M. tristrami	0.9	79.2	±8.3	17.7
	3.5	65.2	±7.9	

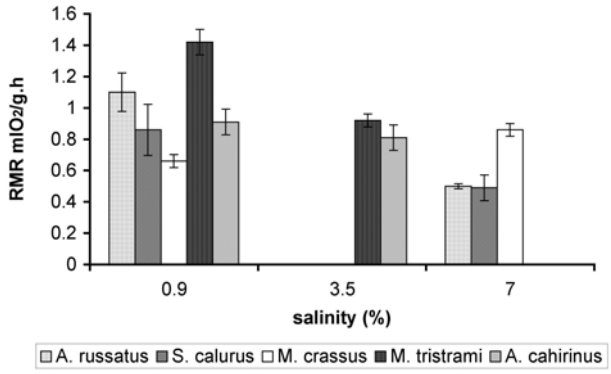

Fig. 1. – Resting metabolic rates RMR ($mlO_2/g.h$) of each studied species under control conditions (0.9% salinity of the water source) and of maximal salinity (3.5% for mesic species and 7% for the xeric ones). Data for *A. russatus* RON & HAIM (2001); data for *S. calurus* PALGI & HAIM (2003); data for *M. crassus* HAIM (UNPUBLISHED); for *M. tristrami* NEUMAN et al. (2000) and data for *A. cahirinus* SCANTLEBURY et al. (2002).

Apart from *M. crassus,* the RMR of all species showed a decrease as the salinity of the water increased (Fig. 1). The VO_2 response to NA increased significantly ($P<0.01$) only in *M. crassus*, when the salinity in the water source was increased (Fig. 2). NST-capacity increased significantly ($P<0.001$) with the rise in salinity only in *A. russatus* and in *S. calurus* (Fig. 3). T_bMin values generally decreased in all species, apart from *S. calurus* ($P<0.05$ for *M. crassus* and $P<0.01$ for *A. russatus*) as a response to the increase in salinity (Table. 3). The sharpest decrease (1.5ºC) was observed in *A. russatus* and the lowest decrease (0.6ºC) in *M. crassus* and in *M. tristrami*. The lowest T_bMin values were measured for *A. russatus* (34.8ºC) under a salinity of 7% of the water source. The highest increase of T_bNA as a response to increase in salinity was observed in *M. crassus*, (1.5ºC) while in some of the studied species as in *A. cahirinus* T_bNA values decreased (1.7ºC) with the increase of salinity in the water source (Table 3).

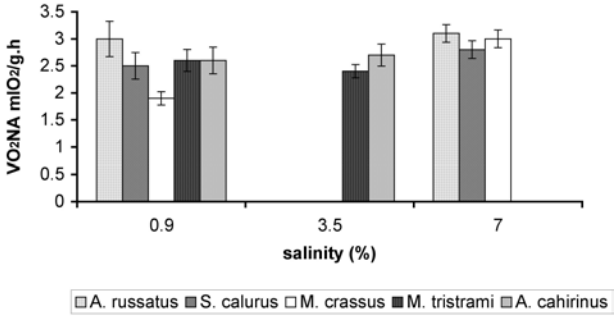

Fig. 2. – The maximal VO_2 ($mlO_2/g.h$) response to noradrenalin injection (VO_2NA) of each studied species under control conditions (0.9% salinity of the water source) and of maximal salinity (3.5% for mesic species and 7% for the xeric ones). Data sources are as in Fig. 1.

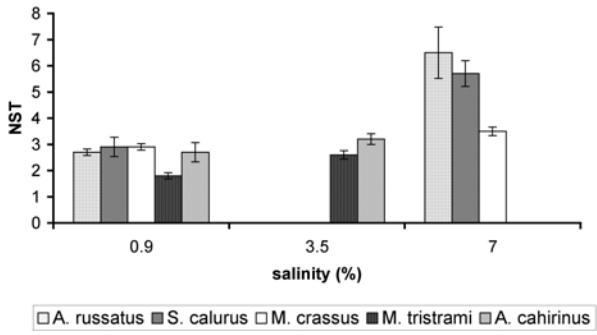

Fig. 3. – Nonshivering thermogenesis NST-capacity (VO_2NA/RMR) of the studied species under control conditions (0.9% salinity of the water source) and of maximal salinity (3.5% for mesic species and 7% for the xeric ones). Data sources are as in Fig. 1.

TABLE 3

Minimal body temperature (T_bMin) and the maximal body temperature response to a noradrenalin injection (T_bNA), maximal urine concentration of each species at control and in maximal salinity of the water source. RMT relative medullary thickness. Values for T_b are taken from RON & HAIM (2001) for *A. russatus*; from SCANTLEBURY et al. (2002) and SHANAS et al. (2003) for *A. cahirinus*; from PALGI & HAIM (2003) for *S. calurus*; from HAIM (UNPUBLISHED) for *M. crassus* and from NEUMAN et al. (2000) for *M. tristrami*. RMT values for *A. cahirinus* are taken from WEISSENBERG & SHKOLNIK (1994) for all other species values are taken from BROSH (1971).

Species	Salinity (%)	T_b Min	T_b NA	Osmolarity	RMT*
A. russatus	0.9	36.3±0.3	38.2±0.8	5353±725	11.4
	7	34.8±1.1	37.8±1.3	9123±3292	
A. cahirinus	0.9	36.7±0.8	37.5±0.3	3006±485	9.3
	3.5	35.0±0.9	35.8±0.7	3389±623	
S. calurus	0.9	37.3±0.2	39.6±0.9	3197±1167	9.03
	7	37.4±0.6	39.7±0.7	7091±1729	
M. crassus	0.9	35.8±0.5	36.8±0.7	2450±830	10.3
	7	35.2±0.3	38.3±0.3	9642±2066	
M. tristrami	0.9	36.8±0.6	38.0±0.5	1500±120	8.2
	7	36.2±0.5	37.7±0.4	3210±523	

* Values are taken from BROSH, 1971; for *A. cahirinus* from WEISSENBERG & SHKOLNIK, 1994.

DISCUSSION

Many desert rodent species show low RMR values (DEGEN, 1997). This physiological trait enables them to conserve water and to keep a balanced heat exchange. In addition, for species that do not engage in reproduction annually as a result of the harsh unpredictable desert conditions, lower RMR values could result as an adaptive longevity trait (HAIM, 1987; HAIM & IZHAKI, 1993). However, in deserts, nights can be cool even during summer. Therefore, increased NST is an important and efficient mechanism for heat production and thermoregulation in a cold environment (HAIM & LEVI, 1990). It was also noted that acclimation to heat or dehydration increases NST-capacity (Fig. 3), compared with control groups at 0.9% salinity (HOROWITZ & SAMUELOFF, 1989; YAHATA et al., 1999; RON & HAIM, 2001).

We show that rock dwelling, desert rodent species such as, *A. russatus* and *S. calurus* can further decrease their RMR values (RON & HAIM, 2001; PALGI & HAIM, 2003), in response to increasing salinity (of dehydrated individuals). In contrast, the soil form burrow dwelling *M. crassus,* a desert adapted species (HAIM & TCHERNOV, 1974), did not reduce it's RMR under the same conditions (Fig. 1). As the thermal refuge for rock dwellers is less efficient than a deep burrow (HAIM et al., 1998), it is proposed that the difference in habitat may play an important role in the thermoregulatory response to dehydration. A decrease in RMR values was noted also in the two mesic species at 3.5% salinity, but these RMR values are much higher than those of the rock dwelling desert adapted species at 7% salinity and are close to those of *M. crassus* at 7% salinity (Fig.1).

The absence of a significant change in VO_2NA, apart from the increase observed in *M. crassus*, suggests that although the response to increased salinity is a reduction in RMR, it seems to have no effect on the response to noradrenalin (Fig. 2). These results tend to suggest that the number and sensitivity of the adrenalin receptors in the brown adipose tissues (BAT) do not change under the current conditions of dehydration, as was suggested by REDLIN et al. (1992) for the difference in thermogenic capacity of juvenile rats.

Food consumption (apparent digestible dry matter intake – ADDMI – and digestible energy) responds to photoperiodic manipulations (HAIM & LEVI, 1990). Yet, the observation that VO_2NA increases in *M. crassus* as a result of dehydration may indicate that decreased food quality, increases the number or affinity of the adrenergic receptors in this species. In addition to a secure thermal refuge, *M. crassus* has an efficient kidney and among the tested desert species, has the highest ability to concentrate its urine at 7% salinity (Table 2). This finding supports the kidney anatomy where the relative medullary thickness (RMT) is high (10.3, BROSH, 1971).

In *S. calurus*, T_bMin does not decrease in response to an increase in salinity. Body temperature is the outcome of two opposite physiological processes, namely heat production and heat dissipation. In *S. calurus* heat production (as reflected by VO_2) decreases and has the same value as *A. russatus*. Yet, in *A. russatus* T_bMin drops at 7% salinity by 1.5ºC. This drop of T_bMin (Table 2) may be a direct result of the decrease in heat production with or without any change in heat dissipation. In *S. calurus* the decrease in heat production with the increase in salinity is accompanied by a decrease in heat dissipation and as a result T_bMin does not decreases. However, in the case of *M. crassus*, T_bMin decreased by 0.6ºC although heat production increased. Therefore, it is suggested that in *M. crassus*, the desert burrow dwelling species, heat dissipation increases with the increasing of salinity.

As both spiny mice are rock dwellers with a poor thermal refuge that use evaporative mechanism for heat dissipation (SHKOLNIK & BORUT, 1969; WEISSENBERG & SHKOLNIK, 1994), the decrease in T_bMin is assumed to be an important contribution for thermoregulation, as it conserves water. In contrast, the bushy tailed gerbil *S. calurus*, shows the same distribution pattern as *A. russatus* and the same habitat, but is nocturnal and digs shallow burrows, which may be used as a thermal refuge (HARRISON & BATES, 1991; PALGI & HAIM, 2003). Under such conditions, it can maintain its T_bMin values even under dehydration conditions, whereas the diurnal *A. russatus* low T_b values, will enable it to forage for longer periods under the hot conditions during day time in its habitat (HAIM et al., 1998).

In conclusion, the results of our study indicate that thermoregulatory mechanisms in different rodent species, respond differently to dehydration caused by a high protein diet and increasing salinity of the water source. Desert species can tolerate higher salinity values, twice those tolerated by mesic species. Thermoregulatory response varies between the different species and is affected by the time of activity (habits) and by the species habitat. The spiny mice of the genus *Acomys* are dependent on their kidneys for survival in the desert since they have a poor thermal refuge and use water for evaporative cooling. This latter phenomenon may indicate that the origin of this genus is from an environment where water was not limited. Therefore, when facing water shortage in xeric environments, spiny mice decrease their T_bMin values and as consequence conserve water.

REFERENCES

BROSH, A. (1971). *Correlation between concentration abilities and kidney structure*. Oranim, School of Education of the Kibbutz Movement (In Hebrew).

DEGEN, A.A. (1997). *Ecophysiology of small desert mammals*. Springer, Berlin.

DEPOCAS, F. & J.S. HART (1957). Use of Pauling oxygen analyser for measurement of oxygen consumption of animals in open circuit system and in short lag, closed circuit apparatus. *J. Appl. Physiol.*, 20 : 388-392.

HAIM, A. (1987). Metabolism and thermoregulation in rodents : are these adaptations to habitat and food quality? *S. Afr. J. Sci*., 83 : 639-642.

HAIM, A. & A. BORUT (1981). Heat production and dissipation in golden spiny mouse *Acomys russatus* from two extreme habitats. *J. Comp. Physiol.,* 142B : 445-450.

HAIM, A. & I. IZHAKI (1993). The ecological significance of resting metabolic rate and nonshivering thermogenesis for rodents. *J. Therm. Biol.,* 18 : 71-81.

HAIM, A. & G. LEVI (1990). Role of body temperature in seasonal acclimatization : Photoperiod-induced rhythms and

heat production in *Meriones crassus*. *J. Exp. Zool.,* 256 : 237-241.

HAIM, A., R.M. MCDEVITT & J.R. SPEAKMAN (1995). Daily variations in the response of wood mice *Apodemus sylvaticus* to noradrenaline. *J. Exp. Biol.,* 198 : 561-565.

HAIM, A. & TCHERNOV, E (1974). The distribution of myomorph rodents in the Sinai peninsula. *Mammalia,* 38 : 201-223.

HAIM, A., R.J. VAN AARDE & N. ZISAPEL (1998). Body temperature daily rhythms in the striped mouse *Rhabdomys pumilio* : The effects of alpha and beta blockade. *Physiol & Behav.*, 63 : 889-893.

HARRISON, D.L. & P.J.J. BATES (1991). *The mammals of Arabia*. 2nd. Ed. Harrison Zoological Museum, Lakeside Printing, Sevenoaks, Kent.

HART, J.S. (1971). RODENTS. In : WHITTOW, G.C., (ed), *Comparative physiology of thermoregulation*, Academic Press, New York.

HELDMAIER, G. (1972). Cold adaptive changes of heat production in mammals. In : SMITH, R.E., (ed), *Bioenergetics International Symposium on Environmental Physiology*, FASEB, MD : 79-82.

HOROWITZ, M. & S. SAMUELOFF (1989). Dehydration stress and heat acclimation. *Prog. Biometeorol.,* 7 : 91-99.

JANSKY, L. (1973). Nonshivering thermogenesis and its thermoregulatory significance. *Biol. Rev.,* 48 : 85-132.

KLEIBER, M. (1961). *The fire of life*. Wiley, New York.

NEUMAN, A., E. RON & O. RAZ-EL (2000). Heat production by nonshivering thermogenesis (NST) in the jird (*Meriones tristrami*) : is it affected by dehydration? *Isr. J. Zool*., 46 : 381 (abstract).

PALGI, N. & A. HAIM (2003). Thermoregulatory and osmoregulatory responses to dehydration in the bushy-tailed gerbil *Sekeetamys caslurus*. *Arid Envir.* (In press)

REDLIN, U., B. NUESSLEIN & I. SCHMIDT (1992). Circadian changes of brown adipose tissue thermogenesis in juvenile rats. *Am. J. Physiol.,* 262 : R504-R508.

RON, E. & A. HAIM (2001). How dehydration affects the thermoregulatory and osmoregulatory abilities of the golden spiny mouse *Acomys russatus*. *Isr. J. Zool.,* 47 : 15-20.

SCANTLEBURY, M., D. AFIK, U. SHANAS & A. HAIM (2002). Comparative nonshivering thermogenesis in adjacent populations of the common spiny mouse (*Acomys cahirinus*) from opposite slopes : the effects of increasing salinity. *J. Comp. Physiol.,* 172B : 1-5.

SCHMIDT-NIELSEN, K. (1964). *Desert animals*. Oxford University Press, Oxford.

SHANAS, U., D. AFIK, M. SCANTLEBURY & A. HAIM (2003). Differential osmoregulatory capabilities of common spiny mouse (*Acomys cahirinus*) from adjacent microhabitats. *J. Zool. Lond.,* 261 : 7-13.

SHKOLNIK, A. (1988). Physiological adaptations to the environment : the Israeli experience. In : YOM-TOV, Y. & E. TCHERNOV (eds), *The Zoogeography of Israel*, Dr. Junk Publishers, The Hague : 487-496.

SHKOLNIK, A. & A. BORUT (1969). Temperature and water relations in two species of spiny mice (*Acomys*). *J. Mammal.,* 50 : 245-255.

SPERBER, I. (1944). Studies on the mammalian kidney. *Zool. Bidr. Uppsala,* 22 : 249-431.

TCHERNOV, E. & Y. YOM-TOV (1988). Zoogeography of Israel. In : YOM-TOV, Y. & E. TCHERNOV (eds), *The Zoogeography of Israel*, Dr. Junk Publishers, The Hague : 1-6.

WEISSENBERG, S. & A. SHKOLNIK (1994). Metabolic rate and water economy in the desert and Mediterranean populations of the common spiny mouse (*Acomys cahirinus*) in Israel. *Isr. J. Zool.,* 40 : 135-143.

YAHATA, T., F. FURUYAMA, T. NAGASHIMA, M. MORIYA, K. KIKUCHI-UTSUMI, T. KAWADA & A. KUROSHIMA (1999). Thermoregulatory responses of the inbred heat tolerant FOK rat to cold. *Am. J. Physiol.,* 46 : R362-R367.

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Spatial distribution of commensal rodents in regions with high and low Lassa fever prevalence in Guinea

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ABSTRACT. Lassa fever is a hemorrhagic fever caused by an arenavirus, which affects approximately 150,000 persons per year in West Africa. It is principally transmitted by rodents of the genus *Mastomys*, which serve as both reservoir and vector of the virus. This study tested the hypothesis that human Lassa fever in Guinea is related to the occurrence rate of the multimammate rat, *Mastomys* spp, inside houses. The analysis was based both on Lassa virus antibody surveys in the human population and the commensal rodent distribution in the same prefectures. The analysis took into account several data sets compiled from the literature (LUKASHEVICH et al., 1993 ; DEMBY et al., 2001) and data from our own ongoing rodent trapping activities in Guinea. The analysis revealed a probable regional gradient of introduced rodent species in houses, with the black rat, *Rattus rattus*, predominating on the coast and the house mouse, *Mus musculus*, predominating approximately 200 km southeast to the coast. The autochthonous species, *Mastomys* spp, were present deep inside the country, from High to Forest Guinea. The regression analysis of *Mastomys* occurrence on human Lassa virus antibody prevalence showed a positive correlation in six administrative regional districts (prefectures) between an increasing *Mastomys* occurrence and increasing seroprevalence. A seventh prefecture, where mainly *M. musculus* occurred, was discordant with this trend, and possible explanations for this divergence are discussed. The partial replacement of *Mastomys* by other species, especially *R. rattus* and *Myomys daltoni*, is discussed as a potential explanation for the low-prevalence of Lassa fever in certain areas.

KEY WORDS : Lassa fever, risk, prevalence, rodent-borne disease, *Mastomys*, occurrence.

INTRODUCTION

Lassa fever is a hemorrhagic fever caused by an arenavirus, which affects approximately 150,000 persons per year in West Africa. In the Republic of Guinea, the activity of Lassa fever varies according to different geographical zones, as determined by human seroprevalence studies. In the northern and coastal regions human antibody prevalences are generally low (3 – 5%), whereas they may be as high as 40% in southern Guinea, close to the borders with Sierra Leone and Liberia (LUKASHEVICH et al., 1993 ; TER MEULEN et al., 1996 ; BAUSCH et al., 2001).

The disease is principally transmitted by rodents of the genus *Mastomys*, the multimammate rats, which serve both as reservoirs and vectors of the virus (SALAZAR-BRAVO et al., 2002), and they might be infected by up to 30% in Lassa-endemic areas (MONATH et al., 1974 ; KEENLYSIDE et al., 1983 ; MCCORMICK et al., 1987 ; DEMBY et al., 2001). Lassa antibodies have been detected in a small number of other rodent species ; however, Lassa virus has rarely been isolated from other genera (WULFF et al., 1975 ; DEMBY et al., 2001) The primary human infections occur in villages, particularly in houses infested by many rodents belonging to this genus as noted by KEENLYSIDE et al. (1983) and MCCORMICK et al. (1987) in Sierra Leone. The principle modes of infection are thought to be exposure to highly infectious urine of chronically infected rodents (rev. in MCCORMICK, 1999) and the direct handling of animals captured for human consumption (TER MEULEN et al., 1996).

Some species such as *M. erythroleucus*, *M. huberti* and *M. natalensis* are distributed in West Africa (BRAMBELL & DAVIS, 1941 ; DUPLANTIER et al., 1990 ; BRITTON-DAVIDIAN et al., 1995 ; GRANJON et al., 1997). Their presence has also been confirmed in Senegal (DUPLANTIER et al., 1990) and in Mali (GRANJON, pers. com.). As their precise identification is difficult, the multimammate rats recently investigated in our study for Lassa virus and antibodies in Guinea were classed as *Mastomys* spp. according to DEMBY et al. (2001) in order to avoid false identifications.

We hypothesised that a high occurrence of *Mastomys* in houses is a possible risk factor of human Lassa fever. To this end, we performed a combined analysis of the literature data and our own data generated during ongoing ecological and genetic studies on commensal rodents to evaluate the eco-epidemiology of Lassa fever in Guinea.

MATERIAL AND METHODS

Background on Lassa virus activity in humans

From 1990 to 1992, Lukashevich and his collaborators conducted a large epidemiological survey of Lassa virus activity in human populations in the Republic of Guinea (LUKASHEVICH et al., 1993). They sampled 25 villages, distributed in different prefectures and established the Lassa virus antibody prevalences based on ELISA. Their results are shown in table 1, where the mean seroprevalences by prefecture were calculated.

TABLE 1

Prevalence of Lassa Virus-specific antibodies by prefecture in Guinea. Adapted from LUKASHEVICH et al., 1993.

Prefecture	Prevalence in % (N°positive/N°tested)
Kindia (Madina Oula)	34 (59/171)
Boffa	4 (6/160)
Boké	5 (5/102)
Pita	6 (10/165)
Labe	7 (8/111)
Mali	5 (9/176)
Faranah	35 (149/420)
Siguiri	11 (45/418)
Guékédou	37 (226/604)
Yomou	27 (119/441)
Lola	28 (102/358)

Background on rodent community

From 1996 to 1997, a team from the Centers for Disease Control (CDC), Atlanta, tested rodent populations in different regions of Guinea for the presence of Lassa virus and antibodies (DEMBY et al., 2001). They investigated 26 villages, distributed in different regions which partially overlap with those of Lukashevich. They captured rodents at 444 house sites and 7 bush sites. As the major part of the rodent collection was made in houses, we considered their results as mainly commensal rodents. Table 2 gives the occurrence rate of *Mastomys*, *Rattus* and *Mus* (percent of total captures) in their trapping. To be concordant with the human data, the rodent data are partitioned by prefecture. In the Kindia prefecture, DEMBY et al. (2001) sampled both the town (60,000 inhabitants) and three villages belonging to the Madina Oula district. To account for the bias of the high occurrence of *Mus musculus* in large towns (DUPLANTIER et al., 1991; DUPLANTIER et al., 1997), the correlation analysis was performed without the data from Kindia town.

TABLE 2

Occurrence of the three main commensal species in villages by prefecture in Guinea, adapted from DEMBY et al., 2001. * Data from Kindia prefecture showing the captures from the town itself were excluded, see text for explanation.

Prefecture	*Mastomys* spp.	*Rattus rattus*	*Mus musculus*
Kindia*	8 (24/295)	9 (26/295)	81 (240/295)
Faranah	94 (271/289)	0	0
Kissidougou	92 (71/77)	8 (6/77)	0
Guékédou	94 (505/536)	5 (25/536)	0
Yomou	94 (505/536)	5 (25/536)	0
Lola	94 (505/536)	5 (25/536)	0

An additional data set obtained from Kedougou in southeastern Senegal by BA (2002) was included in the map presentation. From July 1998 to April 2001, the captures in houses were mainly composed by *Mastomys* spp. (90%; 380/432) and *R. rattus* (9%; 38/432).

Own data on rodent community

Some rodents were collected in houses, distributed in 3 villages on the coastal region, Bamba (10°00'N, 13°53'W, 20 m a.s.l., ±650 inhabitants) and Yafraya (10°05'N, 13°40'W, 20 m a.s.l., ±1600 inhabitants) in October 2002, and Gayebombo (10°08'N, 13°35'W, 86 m a.s.l., ±80 inhabitants) in May 2003. The rodents were trapped with BTS and Ugglan traps in 3-days sessions during October 2002 and with Sherman traps during May 2003. Between four and six traps were set at 30 households. The location of traps was partly directed by the household and variation in building structures. Usually, two traps were set by room, e.g. bedroom, corridors, food storage, or an external kitchen and were baited with a mixture of peanuts, dried fish and wheat flower. Thirty houses were sampled with a total of 456 trap-nights.

In May 2003, an additional village in the Fouta Djallon, Gagal (11°05'N, 12°17'W, 1050 m a.s.l., ±760 inhabitants) was similarly sampled using Sherman traps, where 16 houses were sampled, giving 210 trap-nights.

Data analysis

The analysis proposed here is the combination of data compiled from 1) the human prevalence based on the paper of Lukashevich, 2) the commensal rodent community based on the paper of Demby and 3) our own data based on two recent rodent trapping sessions. To access to the correlation between human Lassa virus prevalence and *Mastomys* occurrence, a simple linear regression analysis was used with the dependent variable being the human prevalence and the independent variable being the *Mastomys* occurrence. Seven prefectures entered into the regression, which was performed with Statview 5, SAS Institute Inc. (1998).

RESULTS

Commensal rodents on the coast and in the Fouta Djallon

The distribution of the commensal rodents according to each sampled village showed that on the coast, *Rattus rattus* was very abundant in large villages such as Bamba and Yafraya, whereas *Mastomys* spp remained the only species in small villages such as Gayebombo (Table 3). To include these data in the analysis, the *Mastomys* occurrence was calculated by combining the collection of the three coastal villages, indicating that *Mastomys* comprised 25% (15/61) of the rodent community. In Fouta Djallon, the *Mastomys* community in houses was 45% (4/9), with the majority of captures identified as *Myomys daltoni*.

TABLE 3

Trapping results from the coastal (Boffa and Dubreka) and the Fouta Djallon (Pita) regions in Guinea. Bamba and Yafraya were sampled in October 2002 whereas Gayebombo and Gagal were sampled in May 2003.

Prefecture	Village	*Mastomys*	*Rattus*	*Myomys*	*Praomys*	*Cricetomys*	*Mastomys* occurrence
Boffa	Bamba	3	20	0	1	0	
Dubreka	Yafraya	0	24	0	0	1	25% (15/61)
	Gayebombo	12	0	0	0	0	
Pita	Gagal	4	0	5	0	0	45% (4/9)

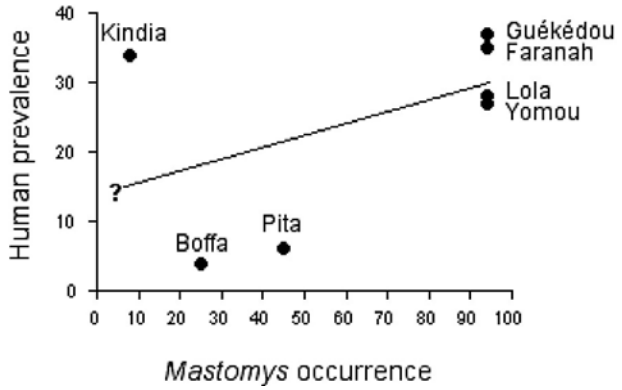

Fig. 1. – Linear regression of percent *Mastomys* occurrence and percent human Lassa seroprevalence in seven prefectures in Guinea. The question mark is related to the unknown epidemiological situation when the *Mastomys* occurrence is null.

Human seroprevalence related to Mastomys occurrence

The regression analysis showed a non-significant coefficient ($r^2 = 0.226$, $p = 0.280$) when the seven prefectures were included (Fig. 1). However, the regression was significant ($r^2 = 0.904$, $p = 0.004$) when Kindia was excluded from the analysis. These results were mapped, indicating missing data related to human seroprevalence or commensal rodents (Fig. 2).

DISCUSSION

Our study on commensal rodents in coastal Guinea and in the Fouta Djallon, combined with the data of Demby, showed that there could be a gradient of introduced species such as *Rattus rattus* and *Mus musculus*, from the coast to the highlands. It is, therefore, suggested to survey inside the country, from the Fouta Djallon to Forest Guinea, to observe autochthonous species such as *Mastomys* spp. and *Myomys daltoni* in households. A *Rattus rattus* gradient has been described by DUPLANTIER et al. (1991, 1997) in Senegal, particularly on the axis between Casamance and the Southeastern region near Kedougou. It is suggested that *R. rattus* is moving further inland with humans and increasing its prevalence with increasing transportation activity and improved infrastructure.

The hypothesis that the Lassa fever risk is directly correlated to the magnitude of the occurrence of *Mastomys* spp. inside houses was partially verified in our analysis. This is also supported by the studies performed in the Tongo Field area in Sierra Leone where 26% (248/953) of humans were Lassa antibody positive and *Mastomys* spp. constituted approximately 80% (311/383) of the captures (KEENLYSIDE et al., 1983). However, this correlation was not observed in the prefecture of Kindia, where three rural villages (Madina Oula, Kagbele and Dar es Salaam) had a high human prevalence of Lassa antibodies (34%) and a low occurrence of *Mastomys* spp. (8%). One explanation for this contradiction could be due to the fact that a Lassa fever outbreak occurred in this region in 1982-83, leading to 137 deaths (BOIRO et al., 1987). The majority of these cases may have originated from human-to-human transmission from the potential introduction of a highly infectious Lassa virus variant. It is, therefore, possible that a high percentage of survivors could still be seropositive in the absence of Lassa virus infected *Mastomys* in the houses. Alternatively, *Mastomys* might have been replaced by *M. musculus*, between the occurrence of the epidemic in the 80s and the study performed by Demby more than 10 years later. This could be due to the intense population movements and traffic between the two countries, particularly during the civil war in Sierra Leone from 1991 to 2002. In such a situation, we can predict that the Lassa fever risk in the Madina Oula zone will decrease if *M. musculus* persists in colonizing the households. It is also possible that contact with infected rodents does not take place in houses but in the fields and bush during hunting of *Mastomys* and other rodents as a food source (TER MEULEN et al., 1996). It is expected that our ongoing investigations will help to understand the eco-epidemiology of Lassa fever in regions with a low prevalence of *Mastomys* spp.

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REFERENCES

BA, K. (2002). *Systématique, écologie et dynamique de populations de petits rongeurs potentiellement réservoirs ou hôtes de virus au Sénégal.* Diplôme de l'Ecole Pratique des Hautes Etudes, Montpellier, 126 p.

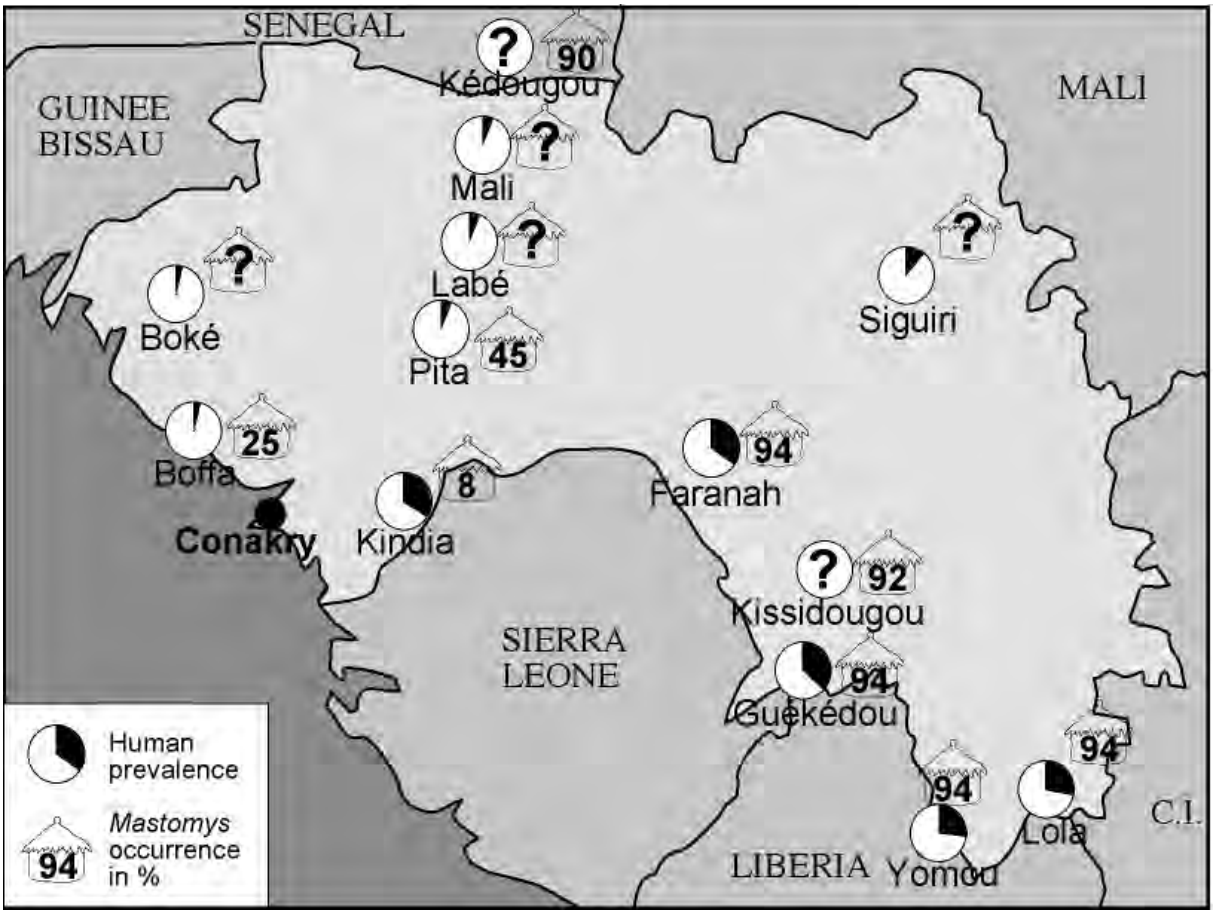

Fig. 2. – Distribution of Lassa virus human prevalence and *Mastomys* occurrence by prefecture in Guinea.

Bausch, D.G., A.H. Demby, M. Coulibaly, J. Kanu, A. Goba, A. Bah, N. Conde, H.L. Wurtzel, K.F. Cavallaro, E. Lloyd, F. Binta Baldet, S.D. Cisse, D. Fofona, I.K. Savane, R. Tamba Tolno, B. Mahy, K.D. Wagoner, T.G. Ksiazek, C.J. Peters & P.E. Rollin (2001). Lassa fever in Guinea : I. Epidemiology of human disease and clinical observations. *Vector Borne and Zoonotic Diseases,* 1 : 269-281.

Boiro, I., N.N. Lomonossov, V.A. Sotsinski, O.K. Constantinov, E.A. Tkachenko, A.P. Inapogui & C. Balde (1987). Eléments de recherches clinico-épidémiologiques et de laboratoire sur les fièvres hémorragiques en Guinée. *B. Soc. Pathol. Exot.,* 80 : 607-612.

Brambell, F.W.R. & D.H.S. Davis (1941). Reproduction of the multimammate mouse (*Mastomys erythroleucus* Temm.) of Sierra Leone. *Proc. Zool. Soc.,* 111B : 1-11.

Britton-Davidian, J., J. Catalan, L. Granjon & J.M. Duplantier (1995). Chromosomal phylogeny and evolution in the genus *Mastomys* (Mammalia, Rodentia). *J. Mammal.,* 76 : 248-262.

Demby, A.H., A. Inapougui, K. Kargbo, J. Koninga, K. Kourouma, J. Kanu, M. Coulibaly, K.D. Wagoner, T.G. Ksiazek, C.J. Peters, P.E. Rollin & D.G. Bausch (2001). Lassa fever in Guinea : II. Distribution and prevalence of Lassa virus infection in small mammals. *Vector Borne and Zoonotic Diseases,* 1 : 283-296.

Duplantier, J.M., J. Britton-Davidian & L. Granjon (1990). Chromosomal characterization of three species of the genus *Mastomys* in Senegal. *Zeitschrift für Zoologische Systematik und Evolutionsforschung,* 28 : 289-298.

Duplantier, J.M., L. Granjon, F. Adam, & K. Ba (1991). Répartition actuelle du rat noir (*Rattus rattus*) au Sénégal : facteurs historiques et écologiques. In : Le Berre M. & L. Le Guelte (eds), *Le rongeur et l'espace*, Editions Chabaud, R. : 339-346.

Duplantier, J.M., L. Granjon & K. Ba (1997). Répartition biogéographique des petits rongeurs au Sénégal. *J. Afr. Zool.,* 111 : 17-26.

Granjon, L., J.M. Duplantier, J. Catalan, & J. Britton-Davidian (1997). Evolutionary systematics in the genus *Mastomys* (Thomas, 1905) (Rodentia : Muridae) : a review. *Belg. J. Zool.,* 127 : 7-18.

Keenlyside, R.A., J.B. McCormick, P.A. Webb, E. Smith, L. Elliott & K.M. Johnson (1983). Case-control study of *Mastomys* natalensis and humans in Lassa virus-infected households in Sierra Leone. *Am. J. Trop. Med. Hyg.,* 32 : 829-837.

Lukashevich, L.S., J.C. Clegg & K. Sidibe (1993). Lassa virus activity in Guinea : distribution of human antiviral antibody defined using enzyme-linked immunosorbent assay with recombinant antigen. *J. Med. Virol.,* 40 : 210-217.

McCormick, J.B. (1999). Lassa fever. In : J.F. Saluzzo & B. Dodet (eds), *Emergence and control of rodent-borne viral diseases*, Elsevier, Paris : 177-195.

McCormick, J.B., P.A. Webb, J.W. Krebs, K.M. Johnson & E.S. Smith (1987). A prospective study of the epidemiology and ecology of Lassa fever. *J. Infect. Dis.,* 155 : 437-444.

Monath, T.P., V.F. Newhouse, G.E. Kemp, H.W. Setzer & A. Cacciapuoti (1974). Lassa virus isolation from *Mastomys natalensis* rodents during an epidemic in Sierra Leone. *Science,* 185 : 263-265.

Salazar-Bravo, J., L.A. Ruedas & T.L. Yates (2002). Mammalian reservoirs of Arenaviruses. *Curr. Top. Microbiol.,* 262 : 25-63.

Ter Meulen, J., I. Lukashevich, K. Sidibe, A. Inapogui, M. Marx, A. Dorlemann, M.L. Yansane, K. Koulemou, J. Chang-Claude & H. Schmitz (1996). Hunting of peridomestic rodents and consumption of their meat as possible risk factors for rodent-to-human transmission of Lassa virus in the Republic of Guinea. *Am. J. Trop. Med. Hyg.,* 55 : 661-666.

Wulff, H., A. Fabiyi & T.P. Monath (1975). Recent isolation of Lassa virus from Nigerian rodents. *B. World Health Organ.,* 52 : 609-613.

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Noki or dassie-rat (*Petromus typicus*) feeding ecology and petrophily

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ABSTRACT. The noki or dassie-rat (*Petromus typicus*) is a rupicolous diurnal herbivore that is endemic to the southwestern arid biogeographical zone of Africa. It is the only representative of the hystricognath family Petromuridae. During our study of the social structure of nokis, we gathered data on their feeding behaviours during four periods totaling nearly seven months from 2000 through 2003.

Nokis fed on a wide variety of plants with a preference for fresh leaves and stems, fruits, and flowers when available. They also ate a wide variety of dry leaves and stems. Relatively few plants and plant parts were avoided. There was no indication that food was cached or stored. There was no evidence that nokis and rock hyraxes (*Procavia capensis*) competed for food resources, despite often feeding together. We speculate that a previously undescribed and unusual noki behaviour (the "tail-stand") is associated with coprophagy.

In hot and arid regions of Australia, some herbivorous mammals feed on the rich flora in rocky areas that is associated with unique water regimes often found in these habitats. A similar relationship may partially explain why nokis are endemic to rocky habitats in the southwestern arid zone of Africa. Other features contributing to the adaptive syndrome include their phylogeny and historical zoogeography, a need for dietary water, a low metabolic rate, a flexible and diverse diet, and an unusual suite of behaviours associated with digestion. The result is an obligate petrophile.

KEY WORDS : Diet, Dassie-rat, Feeding, Namibia, Noki, *Petromus*, Petrophily, Rupicolous

INTRODUCTION

The noki or dassie-rat (*Petromus typicus* A. Smith, 1831) belongs to the monospecific hystricognath family Petromuridae. We prefer the common name “noki” because it avoids the confusion by many people between dassie-rats and rock dassies (rock hyraxes in the mammalian order Hyrcoidea) and true rats (species in the rodent families Muridae and Cricetidae). Noki is derived from a Hottentot dialect (SHORTRIDGE, 1942) and was used by GEORGE & CROWTHER (1981).

Nokis are endemic to Africa in the southwest arid biogeographical region (MEESTER, 1965), where they are closely associated with rocky habitats, especially the Namibian escarpment zone with its numerous mountains, cliff faces, and inselbergs or kopjes (COETZEE, 2002). They occur from extreme southwestern Angola south through Namibia, and into northwestern Cape Province of South Africa. The aridity of the escarpment and closely related Namib Desert is at least 15 million years old (WARD & CORBETT, 1990) and the noki has had an ancient association with these biomes (MEESTER, 1965), as demonstrated by several morphological adaptations to living in rock crevices (GEORGE & CROWTHER, 1981; SKINNER & SMITHERS, 1990). These include a flattened cranium, flexible ribs, and dorso-lateral mammae.

Nokis superficially resemble ground squirrels, including their largely diurnal activity. Apart from general natural history observations (e.g., SKINNER & SMITHERS, 1990) and reports based largely on opportunistic observations (e.g., COETZEE, 1983), there are only two field studies of noki ecology (WITHERS, 1979; GEORGE & CROWTHER, 1981). Recently, reproduction and behaviour of captive nokis have been studied (MESS, 2002).

Because the noki has a limited distribution, there is considerable interest in this near-endemic Namibian family of rodents (GRIFFIN, 1998). In this paper we report information on noki feeding ecology that we gathered while studying the social structure and behaviours of free-ranging nokis in Namibia.

METHODS

Our study was near the Erongo Wilderness Lodge (21º 27.679 S, 15º 52.523 E) on Okapekaha Farm, about 10 km west of Omaruru town in the foothills of the Erongo Mountains. The site is 1240 m above sea level and is characterised by huge rounded granite dikes and domes that rise about 100 m above the surrounding peneplain and smaller 10-20 m high granite outcrops or kopjes (Fig. 1) surrounded by intruding fingers of the surrounding bushveld. The vegetation at the study site is composed of low trees and bushes interspersed with seasonally dense

annual and perennial forbs and perennial bunch grasses. The dominant trees include *Combretum apiculatum*, *Sterculia africana*, *Terminalia prunoides*, and *Boscia albitrunca* and the more dominant bushes included several species of *Grewia*, *Croton gratissimus*, *Dichrostachys cineria*, and *Mundulea sericea*.

Annual mean rainfall at Omaruru Prison is 292.9 mm, with virtually all of this falling during the months of November through April (Fig. 2). Annual average minimum and maximum temperatures are 11.4 and 31.0° C, with May through August being the coolest as well as driest months (Fig. 2).

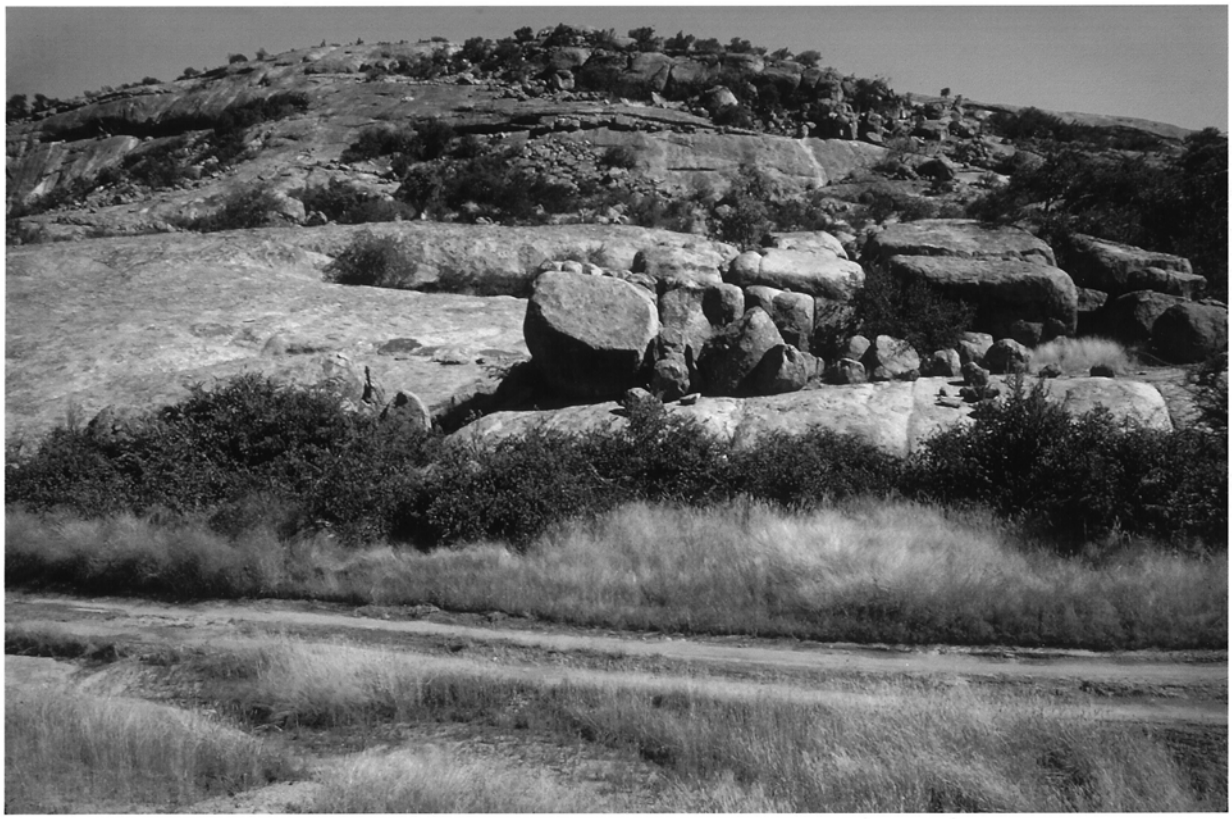

Fig. 1. – Single kopje (3-m-high cluster of boulders in foreground above road) at the Erongo Mountains, Namibia, study site where many of our observations occurred. Note the dense concentration of food plants (mostly *Grewia* spp. and bunch grasses) at the base of the granite rock.

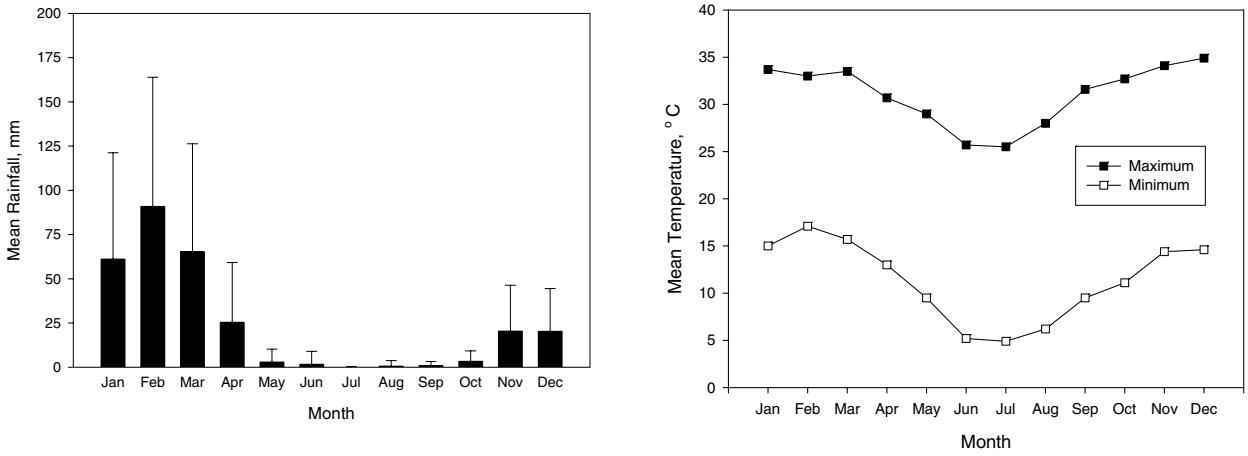

Fig. 2. – Left : Average (40 years) monthly rainfall at Omaruru Prison, located about 10 km from the noki study site. Right : Average (10 years) maximum and minimum monthly temperatures at Omaruru Prison.

It is particularly difficult to catagorise the phenology of arid-land plants because they respond very differently to the high year-to-year climatic variation (HÜSER, 1976). For example, whether and when some perennial plants lose their leaves (generally those classified as "inconsistently deciduous" in Table 1) is closely tied to the occurrence of freezing temperatures and the quantity and timing of the seasonal rainfall. To draw some generalizations about noki feeding ecology, we have subjectively assigned some phenological traits to the common plants at out study site (Table 1), realizing that in some instances this is probably an oversimplification.

TABLE 1

Common plants found at our noki study site (alphabetical order by genus). Those that are especially associated with boulder habitats (e.g., noki habitat) in the Erongo area (personal observations and P. Carven, personal communication) are indicated by an asterisk (*) in the "Traits" column, while those without an asterisk also are commonly found in the surrounding bushveld. Plants not observed eaten by nokis during the 2000-2003 study period are indicated with a dash (--) in the "Parts Eaten" column. In the "Traits" column, we assigned one feature from each of the following groups (separated by commas): perennial (P) or annual (A), deciduous (D) or inconsistently deciduous (I), tree (T) or bush (B) or forb (F) or grass (G). We subjectively ranked each food plant in importance (most = 1 and least = 3) to noki diet based on our observations.

Scientific Name	Parts Eaten	Traits
Abutilon angulatum	Green leaves & stems	P, D, B, 3, *
Abutilon fruticosum	Green leaves & stems	P, D, B, 3, *
Abutilon ramosum	Green leaves & stems	P, D, B, 3, *
Acacia erubescens	Green leaves	P, D, T, 3
Adenolobus garipensis	Flowers	P, I, B, 3, *
Barleria lancifolia	--	P, D, B, *
Barleria sp.	--	P, D, B
Bidens biternata	Entire green plant, dry stems	A, D, F, 2
Blepharis obmitrata	Green leaves	P, D, B, 3
Boscia albitrunca	Flowers	P, I, T, 3
Cardiospermum pechuelii	--	P, D, B
Combretum apiculatum	Dry leaves	P, D, T, 1
Commiphora glaucescens	Dry leaves & stems	P, D, T, 3, *
Croton gratissimus	--	P, D, T, *
Cyphostemma omburense	Green & dry leaves	P, D, F, 1
Dichrostachys cinera	Green leaves	P, D, B, 3
Dombeya rotundifolia	--	P, D, B, *
Dyerophytum africanum	--	P, D, B, *
Enneapogon scoparius	Dry stems	P, D, G, 2
Erythrina decora	--	P, D, T, *
Ficus ilicina	--	P, I, T, *
Forsskaolea viridis	Entire green plant	A, D, F, 1
Grewia bicolor	Green & dry leaves & fruit	P, D, B, 1
Grewia flava	Fruit	P, D, B, 2
Grewia flavescens	Green leaves	P, D, B, 1
Grewia tenax	Green leaves	P, D, B, 1
Helinus integrifolius	Green leaves	P, D, B, 3, *
Hibiscus micranthus	Green leaves & stems	P, D, B, 3
Hibiscus castroi	--	P, D, B
Indigofera filipes	--	P, I, B
Jamesbrittenia pallida	--	P, D, B, *
Lycium basciifolium	Green leaves	P, I, B, 3
Montinia caryophyllacea	Dry leaves	P, D, B, 3 *
Mundulea sericea	--	P, D, B, *
Obetia carruthersiana	--	P, D, T, *
Portulaca sp.	Green leaves	A, D, F, 1
Schmidtia kalahariensis	Dry stems	P, D, G, 2
Solanum rigescentoides	Green leaves	P, D, B, 3, *
Steganotaenia araliacea	--	P, D, T, *
Sterculia africana	Dry leaves, flowers	P, D, T, 2, *
Stipagrostis uniplumis	Dry stems	P, D, G, 2
Talinum arnotii	Green leaves	A, D, F, 1
Terminalia prunioides	--	P, D, T

After determining the suitability of the study site in June 2000 we captured, tagged, and observed four to six nokis during each of four periods : 25 December 2000 through 5 January 2001, 5 September through 21 November 2001, 24 April through 7 July 2002, and 10 May through 26 July 2003. We caught animals with 4.5 x 4 x 15 inch folding aluminium or 16 x 5 x 5 inch single-door wire mesh live traps set during daylight hours and baited with pieces of raw carrots or apples. To prevent hyperthermia in captured animals we positioned traps in the shade or avoided trapping during mid-day.

We attached radio transmitters with collars made of antenna wire inside Tygon tubing (Holohil Systems Ltd., Carp, Ontario, Canada; model MD-2C, 2.2 g weight, 120-day battery life, 20-pound test 10-cm-long wire whip antenna). We radio-located each of the nokis several times a day between 0430 and 2230 hours. When air temperatures were below about 30° C we sat on top of granite boulders and with 8 x 40 binoculars watched tagged as well as untagged nokis. Even with the advantage of being able to always find the radio-tagged animals, observation often was difficult because of obstructing rock, the animals' wariness, and their use of narrow and deep rock crevices for shelter.

RESULTS

The nokis exhibited a catholic diet of plants and plant parts (Table 1), including dry fragments of unidentifiable leaves and stems when fresh plant matter was available. However, some plants appeared to be particularly important in the diet of nokis, perhaps because they were especially common, nutritious, or moist (importance category 1 in Table 1). For example, at the end of the dry season and prior to the rains (September and October, Fig. 2), when nearly 90% of the common plants at our study site were leafless (Table 1), several trees flowered. The nokis often foraged on the surfaces of boulders and the ground under *Sterculia africana* and *Boscia albitrunca* trees where they gleaned fallen flowers. After the main rains (April and May), they foraged on the green leaves, flowers, and fruits of bushes, especially several species of *Grewia* (Table 1). With the approach of the dry season (June and July) nokis focused on plants that still contained moisture, particularly the vine *Cyphostemma omburense* with its fleshy leaves, and annual forbs (e.g., *Forsskaolea viridis* and *Portulaca* sp.) that grew in the deep shade and moist soil at the base of granite boulders. At the height of the dry season (August and September) nokis fed mostly on dry leaf and stem detritus that accumulated at the bases of rock faces and in rock crevices. Although it was difficult to identify these dry plants, we suspect they were the same species that the nokis fed on during other parts of the year.

Another aspect of their habitat is that the plants were highly clumped and the clumps often were composed of different species (Fig. 1). Thus, nokis on one kopje had access to different food plants than nokis on a nearby kopje. For example, the kopje in Fig. 1 lacks several species, most notably the trees *Boscia albitrunca* and *Commiphora glaucescens* and the bushes *Adenolobus garipensis* and *Mundulea sericea*. This spatial variation in species composition made it difficult to determine which plants nokis avoided; we suspect that they actually fed on most plants, even if we only documented them eating 28 out of the 43 (65.1%) most common plants found associated with kopjes in our study area (Table 1). Some plants, however, were only eaten at specific stages in their phenology. For example, the leaves and stems of *Montinia caryophyllacea* were only eaten once they had dried in late July and August. Other plants seemed to be completely avoided, including *Croton gratissimus*, *Jamesbrittenia pallida* and *Indigofera filipes*. Indeed, unlike some of the other plants that we did not see nokis feed on (e.g., *Barleria lancifolia* and *Hibiscus castroi*,), the former three also showed no evidence of being browsed by the other rupicolous mammals on our study site, such as rock hyrax (*Procavia capensis* Pallas, 1780), klipspringer (*Oreotragus oreotragus* Zimmermann, 1783), and Jameson's Rock Rabbit (*Pronolagus randensis* Jameson, 1907). Although we often observed nokis feeding on dry grass stems (Table 1), which were abundant in some areas at the bases of the kopjes (Fig. 1), we did not see them eat or harvest grass seed-heads.

The upper portions of the kopjes that the nokis occupied were virtually devoid of growing plant matter, which required the animals to descend to the base of the rocks to find food (Fig. 1). They often carried single leafed twigs or grass stems (up to about 20 cm long) from the bases of the kopjes to favoured basking and resting spots higher in the rocks, where they fed on the material, including later in the day or on a subsequent day if it was not initially consumed. For example, in late June 2003 at 0655 hrs. one of the collared male nokis moved from the crevice where he spent the night to a crevice at the lower edge of the kopje and began to harvest the green leaves and stems from a *Grewia flaviscens* bush that was about 1.5 metres from his crevice. During the 35-minute feeding bout he made nine trips to the bush, each time bringing back to his crevice a leafed stem, which he ate in his crevice before returning for more. After the feeding bout, he started a session of basking in the sun, which lasted most of the morning. Even though nokis often harvested plants, we found no evidence that this material was actually cached or stored for later consumption.

We never observed or radio-tracked the animals further than about 10 m away from the base of kopjes and rock crevices, where they immediately retreated if disturbed. Although they often climbed into bushes and out onto tree limbs to forage, they usually remained within leaping distance (ca. 1 m) of rocks and safety. The high risk of predation while foraging was illustrated by three of the radio-tagged nokis being killed and eaten at favoured foraging sites. Even though these three different sites were only 2-3 m from the safety of rock crevices at the bases of kopjes, we suspect that the diurnal and solitary black mongooses (*Galerella nigrata* Thomas, 1928), which we often saw hunting in and around our kopjes, surprised and captured the foraging nokis before they could reach the safety of a rock crevice.

We tallied radio locations associated with nokis foraging or harvesting (we did not include instances of plants being ingested after they had been harvested and carried up into the kopje) by daylight quarters between 0600 and 1800 hours in 2001 and 2002. We used the proportion of our radio-tracking effort in each quarter and total feeding bouts to calculate the expected foraging bouts per quarter. These data, starting with 0600 to 0900 hrs., were 20 observed and 10 expected, 4 and 10.5, 4 and 11, and 22 and 18.5. The observed distribution is significantly different from the expected ($X^2 = 9.82$, df = 3, P=0.02), indicating that foraging was concentrated in early morning and late afternoon.

Three times we observed an unusual behaviour by adults that we call a "tail stand" (Fig. 3). These occurred

on flat basking sites and entailed standing on the front feet and propping up the hindquarters with the down-turned and stiffened tail while vigorously kneading or scratching the abdomen simultaneously with both rear feet. Each "tail stand" lasted about 10 seconds. We suspect this behaviour may be related to their feeding habits (see discussion).

Fig. 3. – Adult female noki performing a "tail stand." Drawing based on a photograph of a free-ranging female at a basking site.

Rock hyraxes and nokis often foraged simultaneously in the same *Grewia* bushes, sometimes within 10 cm of each other, but we never saw any agonistic behaviour between the two species. They also used the same basking spots and on 11 occasions we observed single rock hyraxes displace single nokis from these sites. In these cases the approaching rock hyrax either seemed oblivious to the presence of the noki, or it displaced the noki after slowly and cautiously approaching it in a posture that suggested curiosity. In several cases the approach even included an attempt to sniff the basking rodent. In all instances, the noki fled only when the rock hyrax approached very closely, often to within a few centimetres. Although we observed nokis responding to rock hyrax alarm calls by bolting for cover, they did not react to rock hyrax territorial cries. We never had an opportunity to determine whether rock hyraxes responded to the noki "cheeeeeee" alarm call.

DISCUSSION

The diet of nokis was quantified using faecal analyses in the Augrabies Falls National Park on the Orange River in South Africa (GEORGE, 1981) and at Tumasberg, an inselberg in the Namib Desert of Namibia (WITHERS, 1979), which are about 200 km and 950 km south of our Erongo study site. In general, the diet at these two sites was unremarkable; *Petromus* ate a wide variety of plants in rough proportion to their occurrence. However, the dominant plants and diet at the two sites and our study site were different with little overlap in species eaten, which demonstrates the catholic and flexible diet of nokis. Captive nokis also show a wide tolerance for different plant foods (MESS & ADE, this volume).

WITHERS (1979) found little seasonal variation in the diet of nokis, and like nokis at Augrabies Falls (GEORGE, 1981), they ate predominately the stems and leaves of grasses and dicotyledonous plants. Nokis at Erongo seasonally ate different species, as illustrated by their focus on forbs during the wet season (these plants disappeared during the dry season). Also, the diet of the Erongo nokis closely followed the phenology of most plants -- focusing on flowers, then fruits, and then leaves and stems according to the season. It is possible that seasonal differences were not found at Tumasberg with faecal analysis because some tissues (e.g., flowers and fruits) are difficult to detect and there is unlikely to be any significant difference between green and dry leaves of the same species after being digested.

The obvious avoidance by nokis of several plants at our study site (see Results section) is likely due to their containing secondary defence compounds, as evidenced by their strongly aromatic leaves. It is not clear, however, why nokis at all three study sites seemed to avoid grass seed-heads, with their presumed higher energy content compared to leaves and stems.

Nokis, unlike many desert rodents, are not able to rely only on metabolic water (WITHERS et al., 1980) and thus need free-standing water (personal observations; MESS & ADE, this volume) or moisture in plants. Indeed, the importance of water in their diet was shown at Augrabies Falls by their preference for the bases of grass stems, which have a higher water content than tops (GEORGE, 1981). Our study site was more mesic compared to Augrabies Falls and Tumasberg, which average about one half and one third the annual rainfall of our site. Because noki metabolic rate is about 25% lower than the predicted weight-specific rate (WITHERS et al., 1980), perhaps their diet at Erongo was influenced more by the nutritional quality of food plants than by moisture content.

The nokis at Tumasberg ingested a significant amount of insect material (WITHERS, 1979), whereas insectivory was not documented at Augrabies Falls (GEORGE, 1981). We did not observe nokis searching for or eating invertebrates, and captives do not eat insects or meat (MESS & ADE, this volume). It is not clear if insects were ingested inadvertently at Tumasberg, or if they were purposefully eaten in relation to optimal foraging or water needs. In any case, it further demonstrates the flexible diet of nokis.

WITHERS (1979), COETZEE (1983), and MESS & ADE (this volume) describe coprophagy in nokis, and Coetzee also describes captive nokis remasticating food after sitting up on their rear legs and bending their head sharply down to the abdomen and then jerking upright. This "jack knife" motion apparently induces regurgitation prior to remastication. We observed coprophagy and the jack knife action, but only a very few times and we were unable to clearly distinguish the two. Indeed, MESS & ADE (this volume) have not observed regurgitation and remastication in captives and believe that the jack knife action is actually related to male autogrooming of the genitals or possibly masterbation. In any case, if coprophagy and the jack knife behaviours had not been previously described (COETZEE, 1983) we probably would not have recognised them. It is possible that coprophagy occurred more frequently than our observations indicate, especially if it was

performed mainly while animals were hidden from view in rock crevices. Another possibility is that coprophagy and remastication (if it indeed occurs) are related to increasing the efficiency of digesting plant material with a high fiber content (COETZEE, 1983), and are thus more common where coarser plants and plant parts dominate the diet, as may be the case at the more arid Augrabies Falls and Tumasberg study sites. Perhaps the "tail stand" is also related to digestive efficiency -- the aggressive kneading of the abdomen with the rear feet somehow aiding in coprophagy by manipulating or stimulating the digestive track.

At Augrabies Falls, rock hyraxes and nokis do not compete for shelters because they use different sites based on their dissimilar body sizes and the food plants they both use apparently are plentiful enough to avoid competition (GEORGE & CROWTHER, 1981). The lack of food caches by either species also suggests that this resource is not limited. During our study, we observed no agonistic behaviours between the two species at feeding or basking sites, which further supports the absence of competition between the two. Indeed, nokis responded to the alarm calls of rock hyraxes, suggesting that their close spatial and temporal association was mutually beneficial because of increased vigilance for predators.

In hot and dry regions of Australia, some herbivorous mammals are closely associated with rocky habitats because they feed on the particularly diverse and productive flora at these sites (FREELAND et al., 1988). The rich flora is the result of the water concentrating and retaining characteristics of the rocky areas. A similar moisture-related explanation for the vegetative richness of riparian zones is more widely recognised. The bases of kopjes and rock faces at our study site also supported a relatively rich flora. Not only were plants denser at the bases of kopjes, but they seemed to grow taller and remain green longer than in the surrounding bushveld. In addition, there was some evidence of greater species diversity. For example, of the 43 common species found at our noki study site, 19 (44.2%) were especially associated with our kopje habitats (Table 1), while the remainder were more widespread in the surrounding bushveld. Similar patterns in plant communities have been found on other Namibian inselbergs (BURKE, 2002, 2003). We believe the rich flora associated with the bases of kopjes is an important factor in providing an abundant, reliable, and seasonally rich source of food for nokis as well as other rupicolous herbivorous mammals.

CONCLUSIONS

Nokis exhibit a rupicolous adaptive syndrome characterised by several remarkable and inter-related features of their feeding ecology. They are restricted to harsh rocky habitats where their flexible and catholic herbivorous diet is well suited to the rich but clumped, variable, and highly seasonal vegetation. In addition, their low metabolic rate and need for non-metabolic water probably relates to their variable and flexible diet. The unusual behaviours associated with digestion enable them to feed efficiently on plant parts with a high fibre content, which is likely critical during the dry season when nearly all plants have lost their leaves. Nokis have several peculiar morphological adaptations to living in rock crevices that suggest a long association with rocky areas. All these features result in the noki being an obligate petrophile.

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LITERATURE CITED

BURKE, A. (2002). Plant communities of a central Namib inselberg landscape. *Journal of Vegetation Science,* 13 : 483-492.

BURKE, A. (2003). The role of Namibian inselbergs in contributing to local and regional plant species richness. *Biodiversity and Conservation,* 12 : 469-486.

COETZEE, C.G. (1983). The feeding behaviour of *Petromus typicus* A. Smith, 1831 (Rodentia :Petromuridae). *Annales du Musee Royal de l'Afrique Centrale, Tervuren, Belgique, Sciences Zoologiques*, 237 : 203-206.

COETZEE, C.G. (2002). The distribution and breeding seasons of the dassie-rat, *Petromus typicus* (Peteromuridae, Rodentia). *Folia Zoologica*, 51(Supplement 1) : 23-35.

FREELAND, W.J., J.W. WINTER & S. RASKIN (1988). Australian rock-mammals : A phenomenon of the seasonally dry tropics. *Biotropica,* 20 : 70-79.

GEORGE, W. (1981). The diet of *Petromus typicus* (Petromuridae, Rodentia) in the Augrabies Falls National Park. *Koedoe,* 24 : 159-167.

GEORGE, W. & G. CROWTHER (1981). Space partitioning between two small mammals in a rocky desert. *Biological Journal of the Linnean Society,* 15 : 195-200.

GRIFFIN, M. (1998). The species diversity, distribution and conservation of Namibian mammals. *Biodiversity and Conservation,* 7 : 483-494.

HÜSER, K. (1976). Der Niederschlagsgang und die Niederschlagsverteilung im Gebiet des Erongo mittleres Südwestafrika. *Journal of the South West African Scientific Society,* 30 : 7-21.

MEESTER, J. (1965). The origins of the southern African mammal fauna. *Zoologica Africana,* 1 : 87-93.

MESS, A. (2002). *Petromus typicus* : reproductive biology of a poorly known animal. University of Erlangen, Berlin, Germany, *Research Committee Newsletter,* 8 : 38-40.

MESS, A. & M. ADE (2005). Clues on the feeding biology of the dassie rat *Petromus typicus* (Rodentia, Hystricognathi, Petromuridae) derived from a breeding colony. *Journal of Belgian Zoology,* 135 (Supplement) : 43-49.

SHORTRIDGE, G.C. (1942). Field notes on the first and second expeditions of the Cape Museums mammals survey of the Cape Province, and description of some new subgenera and

subspecies. *Annals of the South African Museum,* 36 : 27-100.

SKINNER, J.D. & R.H.N. SMITHERS (1990). *The mammals of the Southern African Subregion*. University of Pretoria, Pretoria, Republic of South Africa. 769 pp.

WARD, J.D. & I. CORBETT (1990). Towards an age for the Namib. In : SEELY M.K. (ed), *Namib Ecology : 25 years of Namib Research. Transvaal Museum Monograph* No. 7. Transvaal Museum, Pretoria, South Africa. 17-26.

WITHERS, P.C. (1979). Ecology of a small mammal community on a rocky outcrop in the Namib Desert. *Madoqua,* 11 : 229-246.

WITHERS, P.C., G.N. LLOUW & J. HENSCHEL (1980). Energetics and water relations of Namib desert rodents. *South African Journal of Zoology*, 15 : 131-137.

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When to live alone and when to live in groups : ecological determinants of sociality in the African striped mouse (*Rhabdomys pumilio*, Sparrman, 1784)

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ABSTRACT. One aim in animal behaviour is to explain why and when animals live in groups. The main approach has been to compare closely related gregarious and solitary species. Here, I discuss data of a medium sized, diurnal muroid rodent, the striped mouse, which demonstrates a high level of intraspecific variability of its social system. In the arid Succulent Karoo, the social structure of the striped mouse is best described as a territorial group living solitary forager with communal breeding and helpers at the nest. Groups can consist of up to 30 adult mice, i.e. four breeding females, one breeding male and their adult offspring. In contrast, the striped mouse is solitary in the mesic grasslands of South Africa, with females inhabiting intrasexually exclusive territories and male territories overlapping those of several females. Association between the sexes is limited to mating, and offspring leave their mother's territory as juveniles. Home ranges in the grasslands are much larger than in the Succulent Karoo. I suggest that the main ecological reasons for these differences in social organization are food abundance, the availability of suitable nesting sites, and the possibility of sun-basking. Whether these ecological differences acted as selection pressures in the past that caused genetic differences and finally speciation (as proposed by a recent study), or whether these ecological differences lead to behavioural differences via an ontogenetic pathway, remains a topic for further research.

KEY WORDS : social flexibility, *Rhabdomys*, striped mouse, ecological determinants of sociality.

INTRODUCTION

The striped mouse (*Rhabdomys pumilio*) is a medium sized (adult body weight 30-70g) muroid rodent, which is active mainly during mornings and afternoons (KRUG, 2002; SCHRADIN & PILLAY, 2004). It is widely distributed in southern Africa, inhabiting many different habitats, such as grasslands, marshes, forests, semi-deserts and deserts (KINGDON, 1974). The social organization of the striped mouse differs dramatically in correlation with the habitat it occupies. In moist grasslands, both sexes have territories that overlap with territories of several individuals of the opposite but not the same sex (BROOKS, 1974; CHOATE, 1972; PERRIN, 1980a; SCHRADIN & PILLAY, 2005 b; WILLAN, 1982; WILLAN & MEESTER, 1989; WIRMINGHAUS & PERRIN, 1993), females raise their young alone, and associations between males and females are only for mating (BROOKS, 1974; WILLAN, 1982). In sum, the striped mouse in the grasslands is a solitary species (SCHRADIN & PILLAY, 2005 b). In contrast, studies conducted in xeric habitats indicate that the striped mouse is a social species here, e.g. in the Kalahari (NEL, 1975; own observ.). A detailed study revealed that the striped mouse is social in the Namib desert, with groups consisting of one breeding female, her offspring that sometimes remain within the maternal territory even after reaching adulthood, and sometimes one adult breeding male that is permanently associated with one female and her offspring, (KRUG, 2002). This is similar to the situation in the Succulent Karoo, a desert in the north west of South Africa, where groups are even larger and more complex (SCHRADIN & PILLAY, 2004). In the Succulent Karoo, groups normally consist of one breeding male, up to four breeding females and their non-reproducing adult offspring of both sexes which remain in their natal territory (SCHRADIN & PILLAY, 2004). Males are permanently associated with groups of breeding females and participate in parental care (SCHRADIN & PILLAY, 2003). However, whereas mice of one group sleep in the same nest, have the same group territory and interact highly amicably with one another, they forage alone (SCHRADIN, published online May 2005, DOI : 10.1007/s10164-005-0158-2) and react highly aggressive towards mice from other groups (SCHRADIN, 2004; SCHRADIN & PILLAY, 2004). These differences in social organization between striped mice from the xeric areas and the moist grasslands lead to the question of whether there is only one single species, *R. pumilio* (WILSON & REEDER, 1993). In fact, there appears outbreeding depression between different populations, which also show assortative mate choice decisions in captivity, i.e. females prefer males of their own population (PILLAY, 2000a; PILLAY, 2000b). An allozyme study of 23 different populations revealed significant differences between populations, with genetic distance being correlated with geographical distance (MAHIDA et al., 1999). Whereas this study suggested the existence of different subspecies, no evidence for different species was found. However, recent studies using mitochondrial DNA proposes the existence of two different species, with *R. pumilio* representing the

social species living in the xeric deserts and semi-deserts, and *R. dilectus* representing the closely related solitary sister species living in the mesic grasslands (RAMBAU & ROBINSON, 2003). These two branches have separated less than three millions years ago and further studies will have to test whether the new species *R. dilectus* will be recognized (RAMBAU & ROBINSON, 2003).

To what extent can genetic differences between social and solitary striped mouse populations explain the observed social differences? An answer to this question is not apparent, but males from the solitary populations in the grasslands show highly-developed paternal care in captivity (SCHRADIN & PILLAY, 2003), for which no evidence exists from the field (SCHRADIN & PILLAY, 2005 b; WILLAN, 1982). Also, there is no difference in paternal response in captivity between males from the Succulent Karoo, where the striped mouse is highly social, and the grasslands (SCHRADIN & PILLAY, 2003). In this paper I discuss how ecological differences between the Succulent Karoo and the grasslands can explain the extreme differences in social organization between striped mice from the two localities. Whether these ecological differences lead to genetic or to ontogenetic differences causing population typical social structures remains hereby unknown.

The Ecological Model

Basic ecological differences

The main difference between the two habitats is the pattern of rainfall. The grasslands in the eastern part of South Africa are a mesic habitat, obtaining more than 1000 mm of rainfall per annum, which occurs mainly during summer (ACOCKS, 1988). In contrast, the Succulent Karoo is an arid habitat, situated in a winter rainfall region, and receives only 50-400 mm rain per annum (ACOCKS, 1988; COWLING et al., 1999) and 160 mm at my field site. Differences in rainfall pattern lead to dramatic difference in plant cover. In grasslands, the entire area is covered by a sea of grasses and herbs, whereas shrubs are the dominant growth form in the Succulent Karoo, with in between open areas inhabited by succulents and in spring wildflowers (COWLING et al., 1999). The Succulent Karoo is rich in endemic plant species (COWLING et al., 1999) and regarded as one of 20 global biodiversity hotspots (MYERS et al., 2000). In the following sections, the ecological consequences of these differences in rainfall and by this vegetation are discussed. The ecological model for the Succulent Karoo is shown in Fig. 1a, for the grasslands in Fig. 1b. Different critical points are marked within the figures, and their importance is outlined below in a chronically order for both habitats.

Succulent Karoo (Fig. 1a)

1) Food abundance is high in spring after the winter rains. Wildflowers are particularly important food resources during spring (unpubl. data), and together with other newly-emerged plant material and insects are important protein sources. Since protein is essential for the onset and maintenance of reproduction (PERRIN, 1980a), breeding occurs during spring and lasts for three months (SCHRADIN & PILLAY, 2005a). Striped mice reach sexual maturity at two months of age (BROOKS, 1982), such that the first pups born during a particular breeding season could reproduce during the season of their birth. However, this would be at the end of the breeding season, with already declining food abundance, and offspring survival may be compromised then. Also, investing energy into reproduction would reduce the survival probability of young parents, since energy could alternatively be invested in somatic development or stored as fat to buffer the effects of poor food supply during summer. (SCHRADIN & PILLAY, 2005 a). This could explain why adult offspring stay at home and invest in personal survival until the next breeding season rather than into reproduction during the season of their birth.

2) Whereas protein rich food occurs primarily during spring, overall food abundance is high throughout the year. The dominant plant species, such as *Zygophyllum retrofractum* shrubs and several succulents are available year round and provide a stable food supply. Nevertheless, the mice show considerable loss in body weight during the hot, dry summer (SCHRADIN & PILLAY, 2005 a). Plant growth starts again in autumn when the rain falls again (COWLING et al., 1999), and food availability improves and reaches a peak in spring. It appears that striped mice in the Succulent Karoo do not need large territories and can share their territories including resources with up to 30 other group members (SCHRADIN & PILLAY, 2004), without experiencing severe competition for food.

3) The patchily distributed plant cover makes it possible for mice to sun bask. In the morning and afternoon, the mice of one group sit together in front of their nest, which is typically situated in a large *Zygophyllum* bush, and warm themselves up in the sun (SCHRADIN & PILLAY, 2004). The time when the sun starts shining on their nest has a significant effect on the initiation of activity (unpubl. data; KRUG, 2002). Sun basking might work as a method of energy saving and as thus leads to reduced demand of food intake, reduced foraging activity and as thus small territory size.

4) Striped mice preferably nest inside dense and thorny *Zygophyllum* shrubs (SCHRADIN & PILLAY, 2004). However, the number of bushes of this species that are big enough for a striped mouse group is limited, and there is strong competition between striped mice and syntopic bush karoo rats (*Otomys unisulcatus*) for access to these nesting sites (SCHRADIN, published online May 2005, DOI : 10.1007/s10164-005-0158-2). As bush karoo rats weigh more than double that of striped mice, they typically win all encounters. The limited number of nesting sites might also promote staying at home at a good nesting site instead of leaving the natal nest and nesting alone at a suboptimal place.

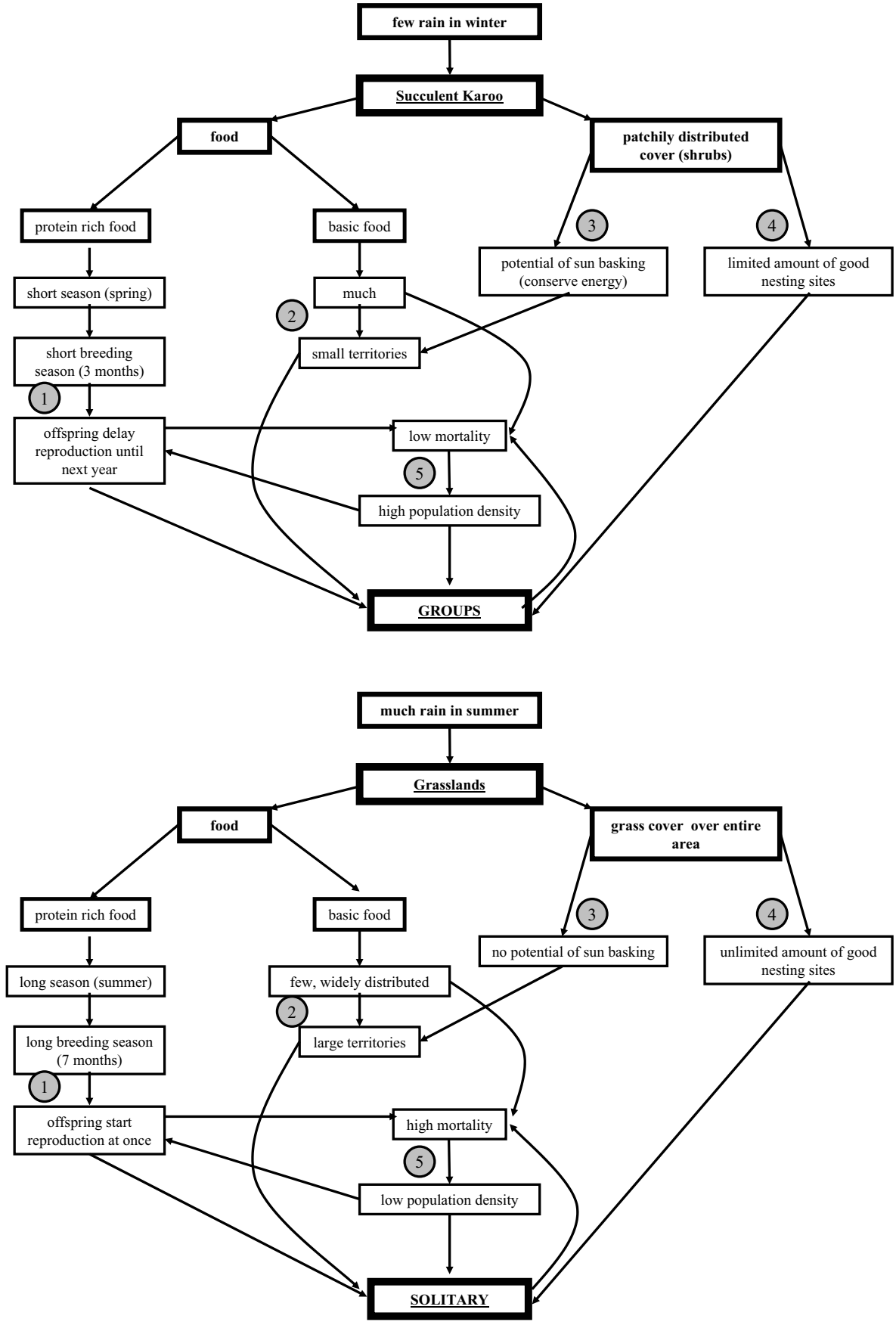

Fig. 1. – A model proposed for the connections between rainfall, protein content of food, food abundance and cover availability, and the social structure of the striped mouse in (a) the Succulent Karoo, and (b) the grasslands of southern Africa. For detailed descriptions see text.

5) Individuals that are present in early summer after the breeding season have a chance of 30% to survive until the next breeding season (SCHRADIN & PILLAY, 2005 a). This survival probability is very high compared to that of grasslands, where it is less than 3% (BROOKS, 1982). It can be explained by the investment of energy into survival instead of reproduction (1), the overall good food supply (2), and benefits of group living. As striped mice in the Succulent Karoo forage alone, but share one nest, benefits of group living must be related to nest sharing : 1. Communal infant care (SCHRADIN & PILLAY, 2004) including paternal care (SCHRADIN & PILLAY, 2003); 2. Thermoregulatory benefits through huddling during the night (ANDREWS & BELKNAP, 1986; CONTRERAS, 1984; temperatures can drop below zero in winter and spring and are even in summer typically below 15 degrees C and thus clearly below the thermal neutral point which might be around 30 degrees, CANALS et al., 1998); 3. Increased vigilance during the night towards potential predators approaching the nest (which is built aboveground using hay). Support for points 2 and 3 is available through unpublished results of videotaping inside two natural nests, in which mice were sleeping closely huddled together, and quickly left the nest during the middle of the night after a disturbance. In conclusion, the high survival probability leads to a high population density of over 50 mice/ha at the start and 200 mice/ha after the breeding season (SCHRADIN & PILLAY, 2005 a). The resulting habitat saturation might then force offspring to stay at home, as no vacant territories are available for emigration.

Grasslands (Fig. 1b)

1) The main protein-rich food sources in the grasslands are grass seeds and insects. These food sources are available throughout the entire spring and summer, and the breeding season stretches over this period of six to seven months (BROOKS, 1974; PERRIN, 1980a; PERRIN et al., 2001). Thus, mice born at the beginning of the breeding season can potentially reproduce in the season of their birth for several months. In the grasslands, mice do not stay at home, but emigrate as juveniles and breeding occurs in young individuals weighing less than 30g (WILLAN, 1982); this does not occurs in the Succulent Karoo (SCHRADIN & PILLAY, 2005 b).

2) Whereas the green grasslands give the impression of high food abundance, this may not be the case. In contrast to other syntopic rodents like vlei rats (*Otomys irroratus*), the striped mouse does not feed on grass (PERRIN, 1980b). Its main food comprises seeds, berries and herbs (CURTIS & PERRIN, 1979; PERRIN, 1980b). These food sources are patchily distributed and scarce. The low abundance of food sources may explain why striped mice have 6 times (females) or even 10 times (males) larger home ranges in the grasslands than in the Succulent Karoo (SCHRADIN & PILLAY, SUBM-B). This difference is even greater when one takes into account that home ranges are exclusive in the grasslands, i.e. overlap only to a small extent with other individuals, but overlap with 5 to 30 other group members in the Succulent Karoo (SCHRADIN & PILLAY, 2005 b). The low food abundance in the grasslands would make it more costly to live in groups, as sharing the territory with other mice that use the same food resources would force territories to become even bigger, thereby increasing the energetic costs of traveling.

3) In the grasslands, the vegetation covers the entire area. Thus, here it is impossible for mice to come out of the cover and perform sun basking to reduce energetic demands by passive warming up. Instead, mice have to increase their body temperature by metabolic heat, for which they have to find more food, and thus need larger territories to fulfill this need.

4) Nest sites in the grasslands are abundant, particularly in areas of dense grass (own observ.).

5) Survival probability of juveniles in the grasslands is only about two months and annual survival probability is only 2.3% (BROOKS, 1974). Low food abundance (PERRIN, 1980b) and low ambient temperatures during winter probably lead to high mortality. Cold weather is a critical factor, as mice are solitary and thus do not benefit from the advantage of huddling in a group. Early dispersal of juveniles is probably another important factor influencing survival probability, as dispersal into unknown habitat is likely to reduce survival probability. Furthermore, young adults do not invest in survival (accumulating resources such as fat to survive the winter), but immediately invest into reproduction. In the grasslands, mice of both sexes start reproducing with a body weight below 30g, whereas in the Succulent Karoo offspring of both sexes remain at home without reproducing, reaching body weights above 40g before reproducing (SCHRADIN & PILLAY, SUBM-B). The low population density, which results from the low survival probability, means that territories are vacant into which offspring can immigrate when reaching adulthood.

DISCUSSION

The model described here is no more than a plausible explanation for the observed patterns of sociality in free-living striped mice. However, it shows associations between abiotic variables (level and season of rainfall), the biotic environment (plant cover, food availability and protein content of food) and social organization in one species (*Rhabdomys pumilio*). Other factors than the ones described in the model might also have effects. One such factor could be predation pressure, which is very difficult to estimate.

A model is only good if it can do two things : First it has to describe the phenomena observed in nature. Above I outlined how the model describes the patterns observed in the Succulent Karoo and the grasslands. One test would be to determine if it also can describe patterns observed in the Namib (described by KRUG, 2002). The main social difference between striped mice in the Succulent Karoo and the Namib is that groups are smaller in the Namib and no cooperative breeding occurs. This is in accordance with the ecological difference that availability of protein rich food is lower (1 in Fig. 1a), but more constant over time (2 in Fig. 1a), such that a clear breeding season is absent (1 in Fig. 1a; KRUG, 2002). As in the Succulent Karoo, good possibility for basking exists (3 in Fig. 1a) and does occur (KRUG, 2002), good nesting sites are extremely limited (4 in Fig. 1a), and the habitat is saturated in the Namib with sometimes extremely high population densities (5 in Fig. 1a), which can explain group

living as a result of the lack of emigration possibilities (KRUG, 2002). Thus, it seems that the model is also suitable for the Namib, although the unique environmental parameters for this habitat would have to be included.

The second prerequisite for the usefulness of a model is that it makes predictions that can be tested. Below I state the predictions made by the model for both habitats, again referring to the important aspects pointed out in Fig. 1. Hereby it is not expected that a single factor will "cause" group living or a solitary lifestyle, but that it is the combination of factors and predictions that are important, as illustrated in Fig. 1.

Predictions in Succulent Karoo

1. Offspring born at the end of the breeding season have a lower survival probability. Heavier mice (i.e. greater body fat) of the same age group have a higher survival probability.

2. Territory size should increase during seasons with poor food supply. In areas with a lower food supply, smaller groups are expected.

3. The body temperature of mice increases significantly when basking (to be measured by implants) and energy expenditure is lower during periods of good sun basking opportunities (summer compared to winter; to be measured by doubled labeled water).

4. Removal of bush karoo rats should lead to striped mice occupying their abandoned nest sites.

5. Low population density leads to a more solitary lifestyle. Removal of groups should lead to adult offspring of other groups leaving their group and taking over these vacant territories.

Many of these predictions might be testable in future. The Succulent Karoo is known to have a low, but highly predictable rainfall pattern (COWLING et al., 1999) and as such predictable food abundance for the striped mouse. However, the Succulent Karoo is currently (2003) experiencing the severest drought since many years. Thus, while my model indicates high survival probability and high population density in the Succulent Karoo, these are unlikely in 2003. This dramatic drought will thus offer the opportunity to study the effects of a reduced population density on the social organization of the striped mouse. It will be possible to test which individuals survived (prediction 1), and it will be interesting to see if there are changes to the social structure (i.e. are the mice solitary, prediction 2 and 5). At the same time, bush karoo rats became nearly locally extinct at my field site, making it possible to test prediction 4.

Predictions in grasslands

1. Mice born at the end of the breeding season should stay longer in their natal territory.

2. Experimental increase of food availability should lead to larger population density (shown by PERRIN & JOHNSON, 1999), smaller home ranges, increased survival probability, and eventually to habitat saturation and finally to a higher level of sociality.

3. Striped mice in warmer grassland habitats (e.g. in the area of Pretoria) should have smaller home ranges than mice in colder grassland habitats (e.g. high in the Drakensberg) because of a lower energy need due to the higher ambient temperature.

4. Providing super-optimal nesting sites should lead to increased sociality. The obvious option for this would be to present nest boxes, but pilot studies with artificial nest boxes were not successful (unpubl. data).

5. Increased survival probability by providing food in the field should lead to a higher degree of sociality, as pointed out in point 3.

CONCLUSIONS

The striped mouse is a convenient model for studying the environmental determinants of sociality. Hereby, it is not of crucial importance, whether the striped mouse is one or two closely related sister species (see Introduction). In this paper, the intention was to point out the ecological differences that explain differences in sociality. Whether these ecological differences acted as selection pressures in the past that caused genetic differences and finally speciation, or if these ecological differences lead to behavioural differences via an ontogenetic pathway, remains a topic for further highly interesting and important research. Further studies should experimentally test the predictions outlined in this paper to test the model described.

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REFERENCES

ACOCKS, J.P.H. (1988). *Veld Types of South Africa*, 3rd edition. Botanical Research Institute, Pretoria.

ANDREWS, R.V. & R.W. BELKNAP (1986). Bioenergetic benefits of huddling by deer mice (*Peromyscus maniculatus*). *Comp. Biochem. Physiol.,* 85 : 775-775.

BROOKS, P.M. (1974). *The Ecology of the Four-Striped Field Mouse,* Rhabdomys pumilio *(Sparrman, 1984), with particular Reference to a Population on the Van Riebbeeck Nature Reserve, Pretoria*. PhD thesis, University of Pretoria, South Africa.

BROOKS, P.M. (1982). Aspects of the reproduction, growth and development of the four-striped mouse, *Rhabdomys pumilio* (Sparrman, 1784). *Mammalia,* 46 : 53-64.

CANALS, M., M. ROSEMANN, F.F. NOVOA & F. BOZINOVIC (1998). Modulating factors of the energetic effectiveness of huddling in small mammals. *Acta Theriologica,* 43 : 337-348.

CHOATE, T.S. (1972). Behavioural studies on some Rhodesian rodents. *Zoologica Africana,* 7 : 103-118.

CONTRERAS, L.C. 1984. Bioenergetics of huddling : test of a psycho-physiological hypothesis. *J. Mamm.*, 65 : 256-262.

Cowling, R.M., K.J. Esler & P.W. Rundel (1999). Namaqualand, South Africa - an overview of a unique winter-rainfall desert ecosystem. *Plant Ecology,* 142 : 3-21.

Curtis, B.A. & M.R. Perrin (1979). Food preferences of the vlei rat (*Otomys irroratus*) and the four-striped mouse (*Rhabdomys pumilio*). *S. Afr. J. Zool.,* 14 : 224-229.

Kingdon, J. (1974). *East African Mammals*. Academic Press, London.

Krug, C.B. (2002). *The behavioural ecology of Rhabdomys pumilio in the Namib Desert.* PhD thesis, Rheinische Friedrich-Wilhelms-Universität Bonn, Germany.

Mahida, H., G.K. Campbell & P.J. Taylor (1999). Genetic variation in *Rhabdomys pumilio* (Sparrman, 1784) : an allozyme study. *S. Afr. J. Zool.,* 34 : 91-101.

Myers, N., R.A. Mittermeier, C.G. Mittermeier, G.A.B.D. Fonseca & J. Kent (2000). Biodiversity hotspots for conservation priorities. *Nature,* 403 : 853-858.

Nel, J.A.J. (1975). Aspects of the social ethology of some Kalahari Rodents. *Z. Tierpsychol.,* 37 : 322-331.

Perrin, M.R. (1980a). The breeding strategies of two co-existing rodents, *Rhabdomys pumilio* (Sparrman, 1784) and *Otomys irroratus* (Brants, 1827). *Acta Oecol.,* 1 : 383-410.

Perrin, M.R. (1980b). The feeding habits of two co-existing rodents, *Rhabdomys pumilio* (Sparrman, 1784) and *Otomys irroratus* (Brants, 1827), in relation to rainfall and reproduction. *Acta Oecol.,* 1 : 71-89.

Perrin, M.R., C. Ercoli & E.R. Dempster (2001). The role of agonistic behaviour in the population of two syntopic African grassland rodents, the striped mouse *Rhabdomys pumilio* (Sparrman, 1784) and the multimammate mouse *Mastomys natalensis* (A. Smith, 1834) (Mammalia Rodentia). *Trop. Zool.,* 14 : 7-29.

Perrin, M.R. & S.J. Johnson (1999). The effect of supplemental food and cover availability on a population of the striped mouse. *S. Afr. J. Wildl. Res.,* 29 : 15-18.

Pillay, N. (2000a). Female mate preference and reproductive isolation in populations of the striped mouse *Rhabdomys pumilio*. *Behaviour,* 137 : 1431-1441.

Pillay, N. (2000b). Reproductive isolation in three populations of the striped mouse *Rhabdomys pumilio* (Rodentia, Muridae) : interpopulation breeding studies. *Mammalia,* 64 : 461-470.

Rambau, R.V. & T.J. Robinson (2003). Molecular genetics of *Rhabdomys pumilio* subspecies boundaries : mtDNA phylogeography and karyotypic analysis by fluorescence *in situa* hybridization (FISH). *Molec. Phyl. Evol.,* 28 : 564-575.

Schradin, C. (2004). Territorial defense in a group living solitary forager : who, where against whom? *Behav. Ecol. Sociobiol.,* 55 (5) : 439-446.

Schradin, C. (published online May 2005, DOI : 10.1007/s10164-005-0158-2). Whole day follows of the striped mouse. *J. Ethol*; 24.

Schradin, C. & N. Pillay (2003). Paternal care in the social and diurnal striped mouse (*Rhabdomys pumilio*) : laboratory and field evidence. *J. Comp. Psychol.,* 117 : 317-324.

Schradin, C. & N. Pillay (2004). The striped mouse (*Rhabdomys pumilio*) from the succulent karoo of South Africa : A territorial group living solitary forager with communal breeding and helpers at the nest. *J. Comp. Psychol.,* 118 (1) : 37-47.

Schradin, C. & N. Pillay (2005 a). Demography of the striped mouse (*Rhabdomys pumilio*) in the Succulent Karoo. *Mammal. Biol.*, 70 : 84-92.

Schradin, C. & N. Pillay (2005 b). Intraspecific variation in the spatial and social organization of the African striped mouse. *J. Mammal.*, 86 : 99-107.

Willan, B.R. (1982). S*ocial ecology of* Otomys irroratus*,* Rhabdomys pumilio *and* Mastomys natalensis*.* PhD thesis, University of Natal.

Willan, K. & J. Meester (1989). Life-history styles of southern African *Mastomys natalensis*, *Otomys irroratus* and *Rhabdomys pumilio* (Mammalia, Rodentia). In : M.N. Bruton (ed), *Alternative Life-History Styles of Animals,* Kluwer Academic Publishers, Dordrecht, pp. 421-439.

Wilson, D.E. & D.M. Reeder (1993). *Mammal Species of the World. A Taxonomic and Geographic Reference*, 2nd edition. Smithsonian Institution Press, Wahingtons D.C.

Wirminghaus, J.O. & M.R. Perrin (1993). Seasonal-changes in density, demography and body-composition of small mammals in a Southern temperate forest. *Journal of Zoology,* 229 : 303-318.

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Movements and spatial patterns of *Mastomys erythroleucus* in maize cropping systems in the Kenyan Rift Valley

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ABSTRACT. We studied movements and spatial patterns of *Mastomys erythroleucus* in four permanent capture-mark-recapture grids in maize cropping systems in the Kenyan Rift Valley. Mean daily movements were affected by maize crop phenology. There was also a significant interaction effect between sex and crop phenology on daily movements. Ranging distances varied by sex with males ranging further than females between successive captures. The majority of marked individuals remained within 20 m of their point of first capture for the three consecutive days in each trapping period. Rodent captures were highly clustered around the grid center or the periphery in three grids but were distributed randomly in the fourth grid. The clustered dispersions could suggest habitat preferences by *M. erythroleucus* within these fields and such areas could provide targets for ecologically based management. Changes in movement patterns in response to environmental factors allow for colonization and use of available resources in cultivated areas. Rodent control measures may focus on, among other approaches, limiting dispersal in farms.

KEY WORDS : Movements; spatial patterns; *Mastomys erythroleucus*; maize cropping systems.

INTRODUCTION

In Kenya, maize is a subsistence crop grown in smallholdings of 0.5 to 20 hectares under partial mechanization (GOVERNMENT OF KENYA, 1997). Such land tenure systems are often under different management practices that lead to the formation of habitat patches across agricultural landscapes (MAKUNDI et al., 1999). In these patches, the qualities of resources including levels of their productivity are frequently ephemeral and follow an annual crop cycle. Species respond to these changes in resource levels over space and time by adopting different life history strategies, especially in their choice of diet, preferred habitat and mating systems (FLEMING, 1979).

Habitat heterogeneity created from resource patches has profound influence on the intensity of the effects of density-dependent factors (such as competition, diseases and predation) on various demographic parameters (GOLDWASSER et al., 1994). Rodents in African fields are highly motile animals (LEIRS et al., 1997) and through dispersal, may connect between patches to reduce the levels of competition for limited resources (STENSETH & LIDICKER, 1992; LAMBIN, 1994; MANSON et al., 1999). Such movements are reflected in their demographic traits such as mortality, recruitment (LARSEN & BOUTIN, 1994), densities, distribution, persistence, extinctions and colonisations (DIFFENDORFER et al., 1995; FERRERAS 2001; THOMAS et al., 2001; BRITO & FERNANDEZ, 2002; JOHNSON et al., 2002; KIE et al., 2002). This may ultimately influence community structure and its biological diversity (HOLT, 1997).

Mastomys erythroleucus (Temminck, 1853), a multimammate mouse, is an important murid pest of maize crops in the Kenyan Rift Valley (ODHIAMBO & OGUGE, 2003). Earlier reports from the area mentioned it as *M. natalensis* (TAYLOR, 1968; TAYLOR & GREEN, 1978), but that species has a different chromosome number. Although documentation of current rodent damages is not available, earlier reports have indicated 20% loss of maize and 34-100% loss of wheat and barley during the 1951 and 1962 rodent outbreaks in western Kenya (TAYLOR, 1968). In the eastern Africa region, the economic importance of this species has been reported from the farmlands in Ethiopia (BEKELE & LEIRS, 1997) while the congeneric *M. natalensis* is the most important pest of maize in Tanzania (MWANJABE et al., 2002). Different strategies for success of pest populations have implications for control. One of the fundamental goals in ecology is to understand the distribution and abundance of organisms and to use this knowledge for the management of populations in a variety of natural and managed ecosystems (GUTIERREZ, 1994). Our study assessed for (i) effects of crop phenology on movement patterns of *M. erythroleucus*; and (ii) its distribution patterns in maize crop fields. We tested the following hypotheses; first, that movement patterns in this species remain unaffected under changing crop phenology in cultivated areas. Secondly, that individuals in this population as in the majority of species are distributed at random.

MATERIAL AND METHODS

Study site

The study was conducted in Rongai Division, Nakuru District, in the Kenyan Rift Valley (35º 28' - 35º 36' E and 0º 13' - 1º 10' S), at altitudes of between 1520-2400m above sea level (Fig. 1). The climate in this area falls between semi-arid (annual rainfall less than 760 mm) in the lower areas and dry sub-humid (annual rainfall of 1270mm) regions in the higher altitudes. Mid-day temperature ranges between approx. 24º-30ºC. The area is important for maize production mainly for subsistence but also as a cash crop. The region contributes substantially to the country's production of maize, beans and potatoes (GOVERNMENT OF KENYA, 1997).

In this study area, the original vegetation of moist forest has been replaced largely by a mosaic of cropped and fallow areas with exotic tree species *Grevillea robusta* and *Cyprus* spp. on the high slopes. In the sub-humid region, the current vegetation has resulted from repeated burning, grazing and cultivation except along moist ravines. The most common ravine tree species were *Podocarpus latifolius*, *Syzygium guineense*, *Ficus stuhlmannii*, *Albizia coriaria* and *Acacia nilotica*. In the intermediate zone, vegetation is dominated by species of *Acacia xanthophloea, Acacia seyal*, *Acacia nubica* and *Acacia senegal*. The common grasses are *Themeda triandra* and *Themeda diplandra*. In the driest part of the Division, the study was carried out near the River Rongai, where the riverine vegetation is dominated by shrubs of *Lantana camara*. Other common species included scattered *Acacia* species, succulents such as *Euphorbia candelabrum*, *Euphorbia tirucalli* and *Aloe ballyi*. The dominant grasses in fallow areas there were *Panicum maximum*, *Cynodon dactylon* and *Themeda triandra*.

Sampling methods

Rodents were live-trapped using Sherman's LFA traps (Sherman Traps Inc., Tallahassee, Florida, USA) on four permanent one-hectare grids coded (i) Mugo, (ii) Beth, (iii) Kurt, and (iv) Moto. The grids were established in April 2000 along an altitudinal gradient from a sub-humid (Mugo grid), over intermediate ares (Beth and Kurt grids) to semi arid (Moto grid) conditions (Fig. 1). Each grid consisted of trapping stations laid at 10 m within and between rows giving a total of 100 stations and marked using white painted bricks. One trap was placed at each station with traps being opened for three consecutive days and nights every 28 days between May 2000 and December 2001. Trapping in Kurt grid commenced in April 2001. Fried coconut cubes mixed with peanut butter and corn oil were used as bait.

Animals were sampled using the Capture-Mark-Recapture (CMR) technique. Captured animals were identified to species level, weighed, sexed and their trapping station and other general remarks were recorded. Each animal was individually marked by toe clipping. The animals were then released at the point of capture and traps re-baited.

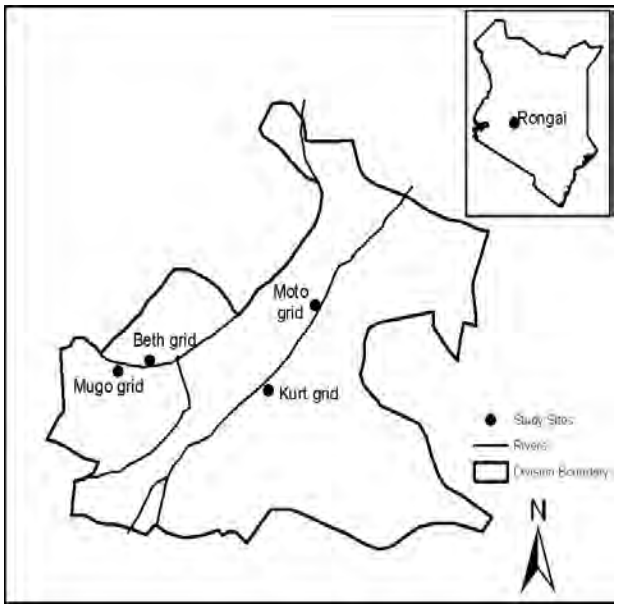

Fig. 1. – A map of Kenya showing the location of Rongai Division and the study grids.

Data analyses

Movements during the trapping periods were determined from the secondary capture histories. The XY reduced capture histories were used in the data input file of the program CAPTURE (REXSTAD & BURNHAM, 2002). Range lengths were determined by calculating the linear maximum distance between capture stations in consecutive months (DELANY & MONRO, 1985), using the formula;

$$d = \sqrt{(x_2-x_1)^2 + (y_1-y_1)^2} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (1)$$

Where d = linear maximum distance estimate (m)
x_1= X-co-ordinate of the initial trap station
x_2= X-co-ordinate of the final trap station
y_1 = Y-co-ordinate of the initial trap station
y_2 = Y- co-ordinate of the final trap station

Daily movement and range length data were first standardized using log (x + 1) transformation (ROHLF & SOKAL, 1984); then General Linear Model (GLM) analysis of variance in program SYSTAT Version 9.0 was used to test the effects of sex, maize crop phenology and grid location on net movements during the trapping period. We did not make appreciable rodent recaptures in year 2000; therefore, these estimates and analysis were based on data obtained between January and December 2001.

Distribution of individuals within maize fields was mapped out using frequency of primary captures in the 100 trapping stations per grid. Only the first capture of each individual in a month was used as the point of reference to eliminate biases. To enable further analysis, the 100 trapping locations were divided into three distinct concentric zones : an outer periphery with 36 trapping stations, middle zone with 28, and a central one with 36 for use in analysis of spatial patterns. Thereafter, a coefficient of dispersion (CD) was calculated for each of the three zones (KREBS, 1989). The significance of the depar-

ture from randomness was assessed statistically by computing :

$$t = \frac{|s^2/\bar{X} - 1.0|}{\sqrt{2/(n-1)}} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (2)$$

where s^2 is the sample variance, $\bar{X}$ is the sample mean capture frequencies and n is the sample size, respectively (CLAPHAM, 1936). The calculated t was compared to the critical values on mathematical tables for n-1 degrees of freedom (ROHLF & SOKAL, 1984).

RESULTS

Movements and range lengths

Daily movement in *M. erythroleucus* was similar (F = 1.39, P = 0.24, n = 204) between sexes across the four grids (mean ± SEM : males= 19.54 ± 1.87 m; females= 17.76 ± 1.41 m) (Fig. 2). Maize phenology affected movements (F = 2.42, P = 0.016, n = 204) as ranging distances varied between planting/seedling (23.6 ± 3.1 m), harvesting (20.1 ± 1.8 m), vegetative (17.6 ± 2.3m), ripening (16.5 ± 4.7 m) and fallow (14.2 ± 2.1 m) stages, respectively. There was also a significant interaction effect (F = 2.76, P = 0.012, n = 204) between sex and crop phenology on these movements during the capture periods. A high proportion (Mugo grid 60.43%, Beth 79.27%, Kurt grid 54.72% and Moto grid 60.00%) of animals moved shorter distances (<20m) between successive capture sessions (Fig. 3).

Range length was significant between sexes (F = 18.972, P < 0.001, n = 136), with males (44.19 ± 3.8 m) ranging further than females (27.54 ± 2.4 m) (Fig. 4). Ranging distances were similar across the grids (F = 1.302, P = 0.276, n = 136). No interactive effect was detected between sex and grids (F = 1.231, P = 0.301, n = 136).

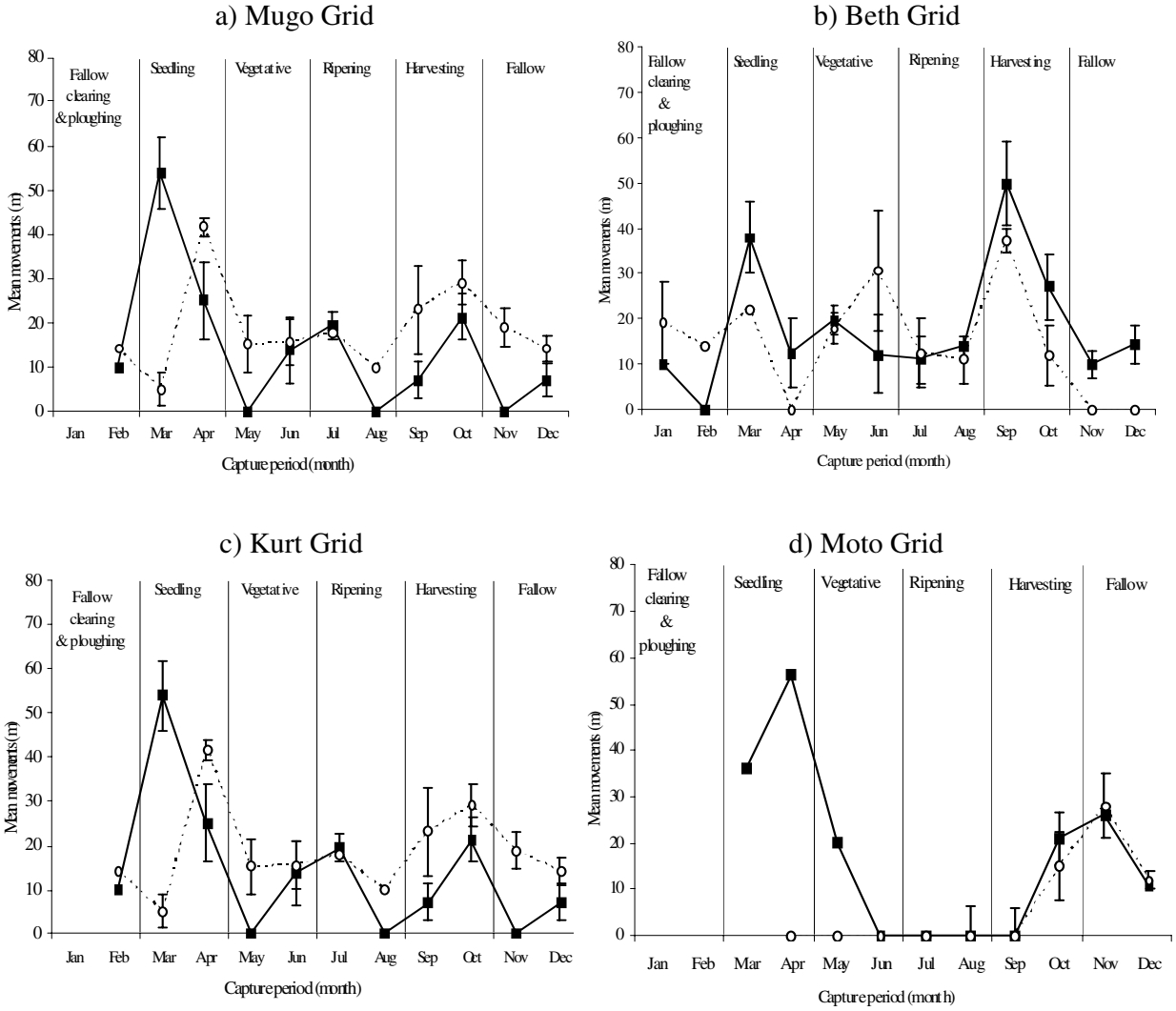

Fig. 2. – Mean (± SEM) daily movement patterns of male (black squares, full lines) and female (open circles, dashed lines) *M. erythroleucus* under different maize crop phenology in; a) Mugo, b) Beth, c) Kurt and d) Moto grids as estimated at 95% confidence interval from XY reduced secondary Capture histories using the program CAPTURE. Data collected from January to December 2001. The different stages of the maize crop fields are indicated.

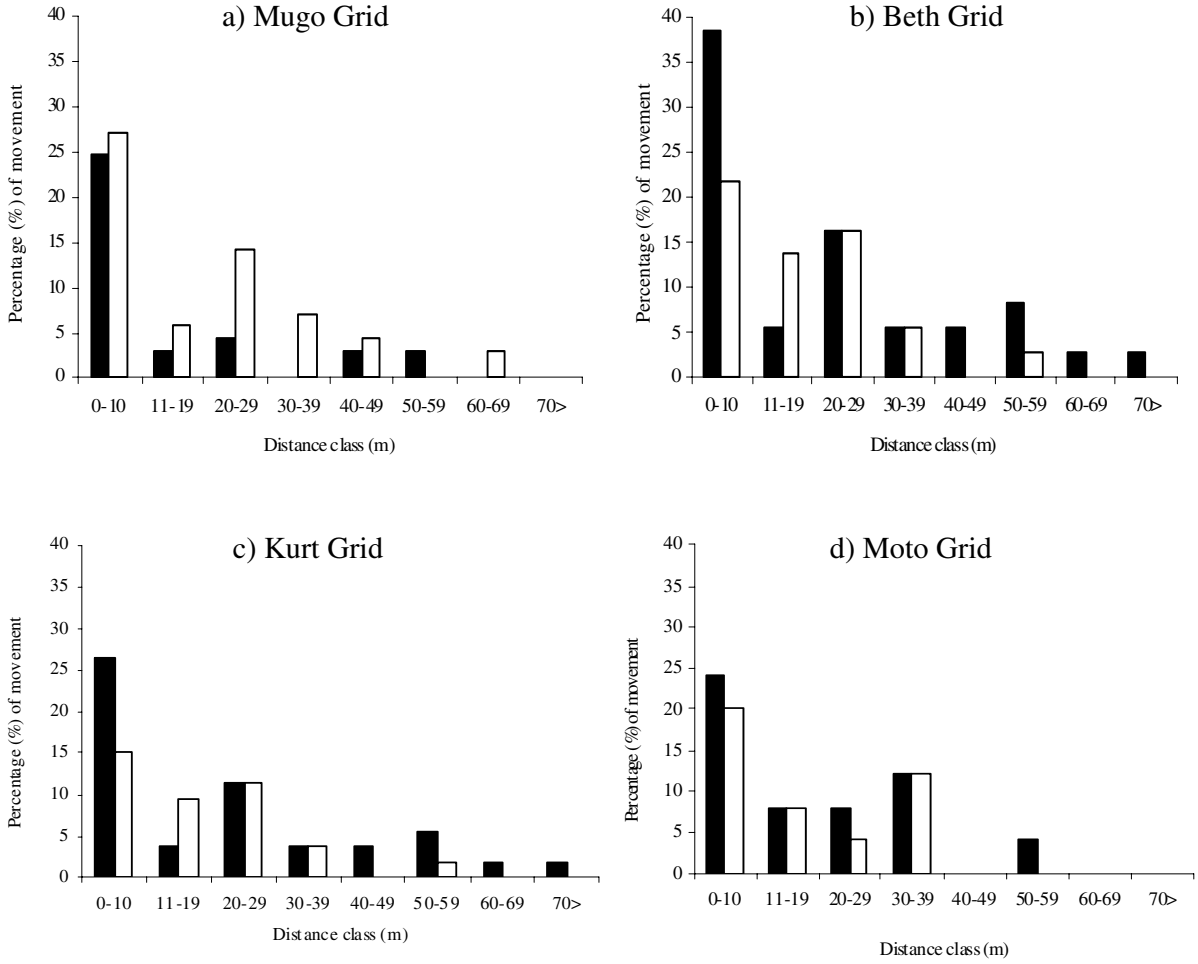

Fig. 3. – Class frequencies of daily movements by adult male (dark) and female (light) *M. erythroleucus* in a) Mugo, b) Beth, c) Kurt and d) Moto grids between successive capture positions following release. Only animals caught within the three sampling sessions are included.

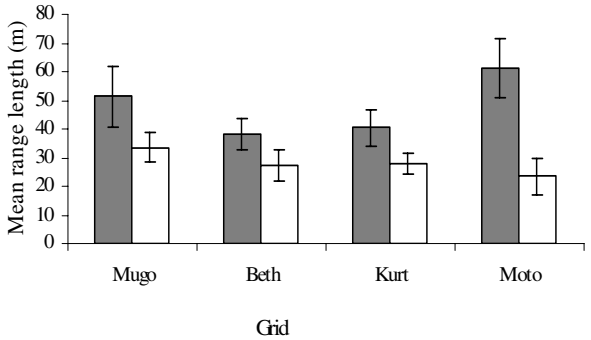

Fig. 4. – Mean range lengths for adult male (dark) and female (light) *M. erythroleucus* between successive capture positions following release.

Distribution of captures within grids

Patterns in rodent distribution were not entirely consistent within the maize fields (Fig. 5). Rodent captures exhibited both peripheral (CD = 1.7, $t = 3.1$, $P < 0.01$, $n = 36$) and central (CD = 1.8, $t = 3.6$, $P < 0.01$, $n = 36$) clustering at Mugo grid. Similar peripheral (CD = 2.5, $t = 6.5$, $P < 0.01$) and central (CD = 1.7, $t = 3.1$, $P < 0.01$) clustering were noted at Beth grid. Distribution in Kurt grid was only clustered peripherally (CD = 2.3, $t = 5.3$, $P < 0.01$, $n = 36$) while it was random at Moto. In Mugo grid, 68.1% of the captures were made from the whole of A-line and along the 5th, 6th, 7th and 8th vertical lines. In the Beth grid, 75.1% of captures were made from the edges of the farm on the J-line and along the 2nd, 3rd, 9th and 10th vertical lines. In Kurt grid captures were mainly from one edge of the farm thus on line-1 and constituting 43.6% of the captures. In Moto grid, no particular trapping stations could be associated with significant proportions of captures.

DISCUSSION

Our study shows that male and female *Mastomys erythroleucus* cover similar distances in their daily activities, i.e. 19. 5 (± 1.9 m) and 17.8 (± 1.4 m), respectively (Fig. 2). However, the long daily movements made during seedling and harvesting stages of maize crop may be due to habitat alterations caused by weeding and trampling on vegetation, respectively, which could have led to reduced ground cover forcing rodents to seek new habitat patches. Manual harvesting could have further reduced food resources in the farms. The short movements during the vegetative, ripening and fallow stages of the crop (Fig. 2),

coupled with the majority of captures (60.43%, 79.27%, 54.72% and 60.00% in Mugo, Beth, Kurt and Moto grids, respectively) less than 20m from point of original capture (Fig. 3) suggests that *M. erythroleucus* settled temporarily within the perimeter of the resource rich habitat patches of the maize farms. Earlier experimental work has shown an inverse relationship between food and rodent movements. Increases in food supplies lead to small home ranges, declined space use and immigration into the area, while the reverse is observed when food supplies are reduced (BOUTIN, 1984). The reasons for the interaction effect between sex and crop phenology, however, remain unclear in this study.

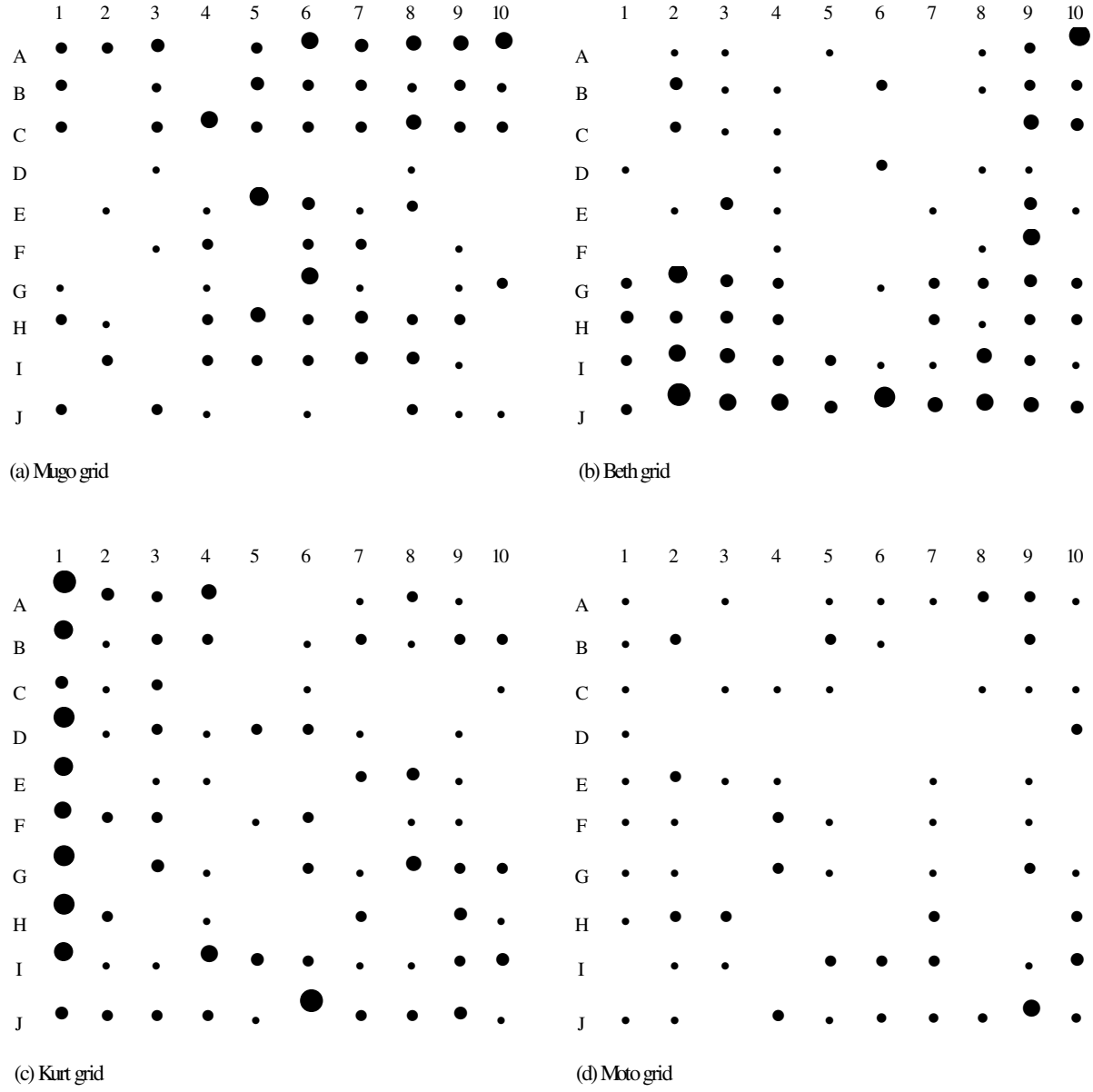

Fig. 5. – Distributions of total capture frequencies per trapping station for *M. erythroleucus* in a) Mugo, b) Beth, c) Kurt and d) Moto grids between January and December 2001.

Although ranging distances were similar between grids, males ranged longer distances than females (44.2 ± 3.8 m and 27.5 ± 2.4 m), respectively (Fig. 4). This would suggest larger home range in males whose larger body size (ODHIAMBO, 2003) suggests a polygynous social system (OSTFELD, 1986). Similarly, a study by MARTIN et al. (1989) in Kitale area in western Kenya captured *M. erthroleucus* up to 50 m from the edges of newly sown vegetation-bare maize fields. The clustering of rodent captures at certain trapping positions (Fig. 5), suggests that some parts of the habitat were utilised more or a possibility of some social attraction that enhanced presence of other individuals. Crops in these loci, for example, at the peripheral and central zones of the farm are likely to suf-

fer increased risk to depredation from rodents leading to the patchy nature of damage. Similar results indicating site fidelity and edge effects have also been reported from the studies of *Arvicanthis niloticus* in Kenyan grassland (Delany & Monro, 1985), and for other small rodents in forest and adjoining farmland habitats (Manson et al., 1999). Conversely, random distribution of captures in Moto may be attributed to pure and uniform stands of fodder grass surrounding the trapping stations. Other studies have reported the influence of microhabitat on food, abundance and distribution of *Mastomys* in Kenyan grasslands (Martin & Dickinson, 1986; Oguge, 1995).

From our study, we can conclude that the crop phenology strongly influenced movements of *M. erythroleucus*. Males generally made wider field excursions than females, but once settled most rodents in the farm preferred to temporarily stay near their home ranges. Changes in movement patterns in response to environmental factors allow for colonisation and use of emerging resources in cultivated areas. Control measures may focus on, among other approaches, limiting dispersal during periods of high precipitation. The clustered dispersions would suggest habitat preferences by *M. erythroleucus* in these fields and this may provide targets for ecologically-based rodent management.

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REFERENCES

Bekele, A. & H. Leirs (1997). Population ecology of rodents in maize fields and grasslands in central Ethiopia. *Belgian Journal of Zoology*, 127 (Suppl.) : 39-48.

Brito, D. & F.A.S. Fernandez (2002). Patch relative importance to metapopulation viability : the neotropical marsupial *Micoureus demerarae* as a case study. *Animal Conservation*, 5 : 45-51.

Boutin, S. (1984). Effect of late winter and food addition on numbers and movement of Snowshoe hare. *Oecologia*, 62 : 393-400.

Clapham, A.R. (1936). Over dispersion in grassland communities and the use of statistical methods in plant ecology. *Journal of Ecology*, 24 : 232-251.

Delany, M.J. & R.H. Monro (1985). Movement and spatial distribution of the Nile rat (*Arvicanthis niloticus*) in Kenya. *Journal of Tropical Ecology*, 1 : 111-130.

Diffendorfer, E.J., M.S. Gaines & R.D. Holt (1995). Habitat fragmentation and movements of three species of small mammals (*Sigmodon, Microtus* and *Peromyscus*). *Ecology,* 76(3) : 827-839.

Ferreras, P. (2001). Landscape structure and asymmetrical inter-patch connectivity in metapopulation of endangered Iberian lynx. *Biological Conservation*, 100 : 125-136.

Fleming, H.T. (1979). Life-history strategies. In : Stoddart D.M. (ed). *Ecology of small mammals*. Chapman and Hall, London : 1-52.

Goldwasser, L., J. Cook & E.D. Silverman (1994). The effects of variability on Metapopulation dynamics and rates of invasion. *Ecology*, 75(1) : 40-47.

Government of Kenya (1997). *Economic Review.* Government Press. Nairobi. Kenya.

Gutierrez, P.A. (1994). A Physiological Based Tritrophic Perspective in Bottom-Up down regulation. *Ecology*, 75 : 2227-2242.

Holt, R.D. (1997). From meta-population dynamics to community structure : some consequences of spatial heterogeneity. In : Hanski I. and M. E. Gilpin (eds). *Metapopulation biology : ecology, genetics and evolution*. Academic Press, San Diego, California, USA : 149-164.

Johnson, R., J.W.H. Ferguson, A.S. Van Jaarsveld, G.N. Bronner & C.T. Chimimba (2002). Delayed responses of small mammal assemblages subject to afforestation-induced grassland fragmentation. *Journal of Mammalogy,* 83 (1) : 290-300.

Kie, G.J., R.T. Bowyer, M.C. Nicholson, B.B. Boroski & E.R. Loft (2002). Landscape heterogeneity at differing scales : effects on spatial distribution of Mule Deer. *Ecology*, 83(2) : 530-544.

Krebs, C.J. (1989). Ecological Methodology. Hapre & Row, Publishers, Inc, New York, NY (664 pp).

Lambin, X. (1994). Natal philopatry, competition for resources and inbreeding avoidance in Townsends' voles (*Microtus townsendii*). *Ecology*, 75(1) : 224-235.

Larsen, K.W. & S. Boutin (1994). Movement, survival and settlement of young red squirrels. *Ecology,* 75(1) : 214-223.

Leirs, H., R.Verhagen, C.A. Sabuni, P.S. Mwanjabe & W.N. Verheyen (1997). Spatial dynamics of *Mastomys natalensis* in a field-fallow mosaic in Tanzania. *Belgian Journal of Zoology*, 127 : (Suppl.) : 29-38.

Manson, H.R., R.S. Ostfeld & C.D. Canham (1999). Responses of a small mammal community to heterogeneity along forest-old-field edges. *Landscape Ecology*, 14 : 355-367.

Makundi, R., N. Oguge & P. Mwanjabe (1999). Rodent Pest Management in East Africa - an ecological approach. In : Singleton, G., H. Leirs, Z. Zhang, and L. Hinds (eds). *Ecologically-based Rodent Management*. ACIAR Publications, Canberra : 460-476.

Martin, G.H.G. & N.M. Dickinson (1986). Small mammal abundance in relation to microhabitat in a dry sub-humid grassland in Kenya. *African Journal of Ecology*, 23 : 223-234.

Martin, G.H.G., N.O. Oguge & J.M. Gatimu (1989). *Technical Report for the Development of Rodent Control Program in the Crop Protection Branch, Ministry of Agriculture, Kenya*. FAO/UNDP Project Ken/85/009.

Mwanjabe, P.S., F.B. Sirima & J. Lusingu (2002). Crop losses due to outbreaks of *Mastomys natalensis* (Smith, 1834) Muridae, Rodentia, in the Lindi region of Tanzania. *International Journal of Biodeterioration and Biodegradation*, 49 : 133-137.

Odhiambo, C. (2003). Population dynamics and habitat use by murid rodents in Maize cropping systems in Rongai Division, Nakuru District, Kenya. M.Sc Thesis, Kenyatta University, Nairobi.

Odhiambo, C. & N.O. Oguge (2003). Patterns in rodent pest distribution in a maize cropping system in the Kenyan Rift Valley. In : Singleton, G., L.A. Hinds, C.J. Krebs & D.M. Spratt (eds). *Ecologically-Based Rodent Management*. ACIAR Publications, Canberra : 217-219.

Oguge, N.O. (1995). Diet, seasonal abundance and microhabitats of *Praomys (Mastomys) natalensis* (Rodentia : Muridae) and other small rodents in a Kenyan sub-humid grassland community. *African Journal of Ecology,* 33 : 211-223.

OSTFELD, R.S. (1986). Territoriality and mating systems of California voles. *Journal of Animal Ecology*, 38 : 341-359.

REXSTAD, E. & K. BURNHAM (2002). Users' guide for interactive program CAPTURE. Abundance Estimation of Closed Animal Populations. Internet : *ftp ://pwrcftpr.er.usgs.gov/research/software/capture.zip.*

ROHLF, F.J. & R.R. SOKAL (1984). Statistical tables. 2nd ed. W. H. Freeman and Co., San Franscisco.

STENSETH, N.C. & W.Z. LIDICKER JR. (1992). Pre-saturation and saturation dispersal 15 years later : some theoretical considerations. In : STENSETH and W. Z. LIDICKER JR. (eds). *Animal dispersal* : *Small mammals as a model.* Chapman and Hall, London : 199-220.

TAYLOR, K.D. (1968). An outbreak of rats in agricultural areas of Kenya in 1962. *East African Agricultural and Forestry Journal*, 34 : 66-77.

TAYLOR, K.D. & G. M. GREEN (1978). The influence of rainfall on diet and reproduction in four African rodent species. *London Journal of Zoology*, 174 : 453-471

THOMAS, J.A., N.A.D. BOURN, R.T. CLARKE, K.E. STEWART, D.J. SIMCOX, G.S. PEARMAN, R. CURTIS & B. GOODGER (2001). The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proceedings of the Royal Society of London*, 268 : 1791-1796.

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Influence of variations in land use intensity on species diversity and abundance of small mammals in the Nama Karoo, Namibia

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ABSTRACT. The influence of the intensity of land use on small mammals in the ecoregion Nama Karoo, Namibia was investigated within the biodiversity programme BIOTA. Changes in species diversity and abundance were investigated across a fence separating heavily grazed communal and lightly grazed government owned rangeland. Assessing and monitoring of the small mammal populations were done seasonally from 2001-2003 on each of 2ha plots by using capture-mark-recapture methods. In total, 311 individuals representing nine species were caught within 5760 trap nights. Species richness, total abundance, species diversity and settlement was lower in the overgrazed area. The most abundant species were the Gerbillinae, *Gerbillurus vallinus* and *Tatera leucogaster. T. leucogaster* did not occur in the overgrazed area. Due to the loss of grass cover, smaller bush diversity, bush encroachment and smaller arthropod abundance in the overgrazed area, changes in the small mammal community were most likely caused by the loss of food resources, available dew, disruption of habitat structures, cover and shelter and by increased predation risk. Only the 'desert' species, *G. vallinus,* was favoured by the degraded land. It is also obvious that the uncontrolled grazing in the communal lands has affected the biodiversity and the regeneration potential, thus leading to land degradation.

KEY WORDS : Namibia, Nama Karoo, fence-line contrast, land use, rodent ecology, *Gerbillurus, Tatera.*

INTRODUCTION

Small mammals are important components of arid and semi-arid ecoregions : as consumers (KERLEY, 1992a), predators and dispersers of seeds (PRICE & JENKINS, 1986), burrowers and as prey for carnivores and raptors (KOTLER, 1984; HUGHES et al., 1994). Changes of habitat structure and complexity are associated with changes in small mammal community structure and species richness (DELANY, 1964; ROSENZWEIG & WINAKUR, 1969; BOND et al., 1980; GRANT et al., 1982; ROWE-ROWE & MEESTER, 1982; KOTLER, 1984; ABRAMSKY, 1988; KERLEY, 1992b; ELS & KERLEY, 1996; HOFFMANN, 1999; AVENANT, 2000).

Large herbivores can modify the vegetation layer in terms of structure and species composition to a level where small mammals are affected (BOWLAND & PERRIN, 1989; KEESING, 1998; HOFFMANN, 1999). An ecological disturbance of the habitat is often associated with decreases in small mammal diversity. Therefore biodiversity of small mammals can be used as an indicator of disturbance in an ecosystem.

Most of the Karoo ecoregion in Namibia is rangeland for livestock grazing (HOFFMAN et al., 1999) and heavy grazing has left parts seriously degraded (LLOYD, 1999). Livestock grazing has been identified as the major threat to biodiversity in that region, but also mining, agriculture and alien invasive plants are significant threats (LOVEGROVE, 1993; LLOYD, 1999). In general most investigations on the effects of grazing in rangelands have centred on vegetation (NOY-MEIR et al., 1989; OLSVIG-WHITTAKER et al., 1993; TODD & HOFFMAN, 1999); with only a few studies on how the extent of grazing influences arthropod assemblages (DEAN & MILTON, 1995; RIVERS-MOORE & SAMWAYS, 1996; SEYMOUR & DEAN, 1999; HOFFMANN et al., 2003). Investigations on the effect of different land use practises on small mammal assemblages in Africa are scanty (KERLEY, 1992b; NYAKO-LARTEY & BAXTER, 1995; MONADJEM, 1999).

The aim of this study was to determine the influence of different land use intensities on the diversity of small mammals. Within the interdisciplinary biodiversity programme BIOTA (Biodiversity Monitoring Transect Analysis in Africa; cf. ZELLER, 2003) a study on the population ecology of small mammals has been carried out in the Nama Karoo, southern Namibia. This study was carried out in the heavily grazed communal rangeland and a neighbouring moderately grazed rangeland, used for Karakul breeding purposes, to address the following questions :

(1) Does small mammal species richness, abundance and diversity differ between overgrazed and moderately grazed areas?

(2) Does heavy grazing influence the composition of small mammal assemblages?

(3) Which species, if any, are most affected by the habitat changes? Does it favour any species?

MATERIAL AND METHODS

Study area

The Nama Karoo occurs on the central plateau of the Cape Province in South Africa, and extends over the Orange River into Namibia in the northwest, where the study was conducted. This ecoregion is described as a vast, open, arid region dominated by grassy dwarf shrubland with summer rain and climatic extremes, where droughts are common (VENTER et al., 1986; DEAN & MILTON, 1999). Most of this ecoregion is rangeland for livestock grazing (HOFFMAN et al., 1999); less than one percent of the Nama Karoo is protected (COWLING, 1986; BARNARD et al., 1998). The region is characterized by fence-line-contrasts caused by varying land use practises.

Fig. 1. – **Fence-line-contrast of the study sites.** Left : overgrazed communal farming area of Nabaos; right : moderately grazed governmental farming area of Gellap-Ost.

The study was conducted on two neighbouring areas with different land use practises (Fig. 1), approximately 20km northwest of Keetmanshoop. One study plot was highly overgrazed, mainly by goats within Nabaos communal area (26°23'26"S, 17°59'43"E). The other plot (distance 1.5km) was within the government Karakul sheep breeding farm in Gellap-Ost (26°24'04"S, 18°00'17"E). In contrast to the uncontrolled grazing in Nabaos, Gellap-Ost uses a rotating grazing system with a lower stocking rate. Free-ranging ungulates like Kudu (*Tragelaphus strepsiceros*) and Steenbok (*Raphicerus campestris*) were rarely observed.

There are three main seasons : hot/wet (January-April) cold/dry (May-August) and hot/dry (September-December). Rainfall occurs in summer from January to April and averages 150mm per year (cf. MENDELSOHN et al., 2002). In 2002 rainfall averaged 178mm, but in 2003 there was drought, with only 55mm of rainfall. The mean monthly temperature range was 2002 22°-37°C (maximum) and 8°-20°C (minimum).

Trapping

Trapping was conducted on two 2ha grids which were separated by a fence and 1.5km apart. Each grid consisted of 90 Sherman standard live traps spaced by 15m intervals. Capture-mark-recapture methods (CMR) were used during trapping sessions of 4 consecutive trapping nights in each plot. The investigations took place at different seasons per year. Traps were baited with a mixture of peanut butter, oats, mashed bananas and bird seeds. These were set before sun set, checked at night and in the morning. In the second study year, day trapping was done in addition. Captured animals were weighed, sexed and body measurements and reproductive status were recorded. Each animal was individually marked by using a subcutaneous tattoo on the underside of the tail's base (HUGO, 1990; cf. HOFFMANN, 1999).

Data analysis

The term ‘trap night' is used to describe one trap which was set for a 24h period (ROWE-ROWE & MEESTER, 1982). Trap success was calculated as the number of captured individuals/100 trap nights. Abundance was used because it differed only by 1.2% from the Minimum Number Alive (MNA) (cf. BRONNER & MEESTER, 1987). For species diversity calculations the Shannon Wiener diversity index (Hs) was chosen. For survival calculations, new individuals of the last trapping session were not considered. Those which were trapped only in one trapping session, ‘survived’ at least for one week.

Assessing and monitoring environmental features

For understanding the interrelation between small mammal coenosis and their habitat different environmental features were assessed and monitored. Data on rainfall and temperature were given by a BIOTA computer controlled weather station near the Gellap-Ost observatory. Bushes were counted, their sizes estimated in four categories between ∅ 0.5 - ≥2.0m and mapped. Ground vegetation cover per plot was estimated within ten 4m²-frames by using the Londo-scale (LONDO, 1975) and then extrapolated. Also plant phenology was monitored over the study period. Arthropod sampling was done using 10 pitfalls per plot over 8 days, to assess and monitor changes of epigaeic arthropod abundance (cf. VOHLAND et al., 2005). Small mammal burrows were counted and mapped once in both plots in October 2002. Observations of potential small mammal predators were recorded.

RESULTS

Habitat features of the study plots

In Nabaos, no grass layer existed all year round. In Gellap-Ost the dominant grass species *Stipagrostis uniplumis* (height app. 50cm) covered the ground by up to 10%. Herbs occurred mainly after the rain. Bush cover was generally low (Nabaos : 2.5%, 488m^2, 1382 ind.; Gellap-Ost : 2.1%, 415m^2, 685ind.). More large bushes (∅ ≥1.5m) were found in Gellap-Ost, where bushes covered an area 1.6 times larger than that in Nabaos. *Rhigozum trichotomum* was the dominant bush in both plots, whereas *Catophractes alexandri* and *Calicorema capitata* were the subdominant species in Gellap-Ost, and Nabaos respectively. Both *Boscia foetida* and *Phaeoptilum spinosum* were also abundant in both plots. Bush diversity was lower in Nabaos (Hs 0.96) than in Gellap-Ost (Hs 1.28).

All burrows were located in bushes in Nabaos, whereas only 61% were in bushes in Gellap-Ost. The rest of the

burrows were in the open grassland. Twelve percent (out of 25) and 37% (out of 90) of the burrows were occupied by small mammals in Nabaos and Gellap-Ost respectively.

In total, within 1280 trap nights 16713 epigaeic arthropods in 19 orders (without mites and collembola) were collected and were composed mainly of ants, with 9466 specimens, beetles with 1673 specimens, and termites, with 747 specimens. Most animals were trapped in May in both years, after the rainy season. In Nabaos the arthropod activity was lower and only 38% of the ground active arthropods were trapped.

Potential predators of small mammals in the area were the Spotted Eagle Owl (*Bubo africanus*), Pale Chanting Goshawk (*Melierax canorus*), Black-backed Jackal (*Canis mesomelas*), Bat-eared Fox (*Otocyon megalotis*), Cape Fox (*Vulpes chama*), Caracal (*Felis caracal*), mongooses and various species of snakes.

Species richness

Between October 2001 and August 2003, eight trapping sessions per plot were conducted. Out of a total of 5760 trap nights, 311 individuals (911 captures) representing nine species were caught and marked (Table 1). The mean species richness in Nabaos was 3.3 (range : 2-6) and in Gellap-Ost 5.4 (range : 4-6) (Fig. 2). The mean monthly trapping success was 4.79 $\pm$ 2.33 for Nabaos and 10.42$\pm$ 6.32 for Gellap-Ost. The overall trap success in Nabaos out of 2880 trap nights was 3.75 and 7.05 in Gellap-Ost.

TABLE 1

Species richness
Listed are all captured species and the total of recorded individuals within 5.760 trap nights.

per plot 2880 trap nights	Nabaos		Gellap-Ost	
	ind.(n)	%	ind.(n)	%
Macroscelididae				
Elephantulus intufi (A. Smith, 1836)	**1**	0.92	**9**	4.46
Muridae >Gerbillinae<				
Desmodillus auricularis (A. Smith, 1834)	**10**	9.17	**3**	1.49
Gerbillurus vallinus (Thomas, 1918)	**80**	73.39	**44**	21.78
Gerbillurus paeba (A. Smith, 1836)	**1**	0.92		
Tatera leucogaster (Peters, 1852)			**118**	58.42
>Murinae<				
Aethomys namaquensis (A. Smith, 1834)	**1**	0.92	**13**	6.44
Mus indutus (Thomas, 1910)			**2**	0.99
Rhabdomys pumilio (Sparrman, 1784)	**12**	11.01	**4**	1.98
Saccostomus campestris (Peters, 1946)	**4**	3.67	**9**	4.46
total individuals	109		202	
Σ captures	282		629	

The overall species richness and abundance was lower in Nabaos than in Gellap-Ost, which is also expressed by the diversity index (Hs) : Nabaos (Hs 0.95; 7 species, 108 individuals.), Gellap-Ost (Hs 1.29; 8 species, 203 individuals). The main species were the gerbils, *Gerbillurus vallinus* (Thomas, 1918) and *Tatera leucogaster* (Peters, 1852). It was striking, that *T. leucogaster* was not recorded on the Nabaos plot. *Mus indutus* (Thomas, 1910) was only trapped in Gellap-Ost, but was also observed once in Nabaos. *Crocidura sp*. was found in owl pellets of *Bubo africanus,* collected in the farming area of Gellap-Ost during the study period, (pers. communication MIKE GRIFFIN, Namibia 2003).

Abundance and diversity

In Nabaos, species diversity and total abundance (3-29 individuals/2ha) was lower than in Gellap-Ost (12-75 individuals/2ha). In both plots, the highest recruitment was found in August 2002 due to the high reproduction activity during the rainy season, followed by decrease of total abundance in October 2002. *G. vallinus* was the dominant species in Nabaos, and only subdominant in Gellap-Ost, where population density fluctuated highly (Fig. 2).

T. leucogaster was the dominant species in Gellap-Ost, with a composition of 33-72% of the total abundance (Fig. 2b). In August 2003, when the abundance of *T. leucogaster* was lowest, the proportion of other species was highest, which is also shown by a high diversity index (1.47). Although fewer species were recorded per trapping session in Nabaos (Fig. 2) compared to Gellap-Ost, there was an overlap in the species occurring in the two plots (Table 1).

Settlement and survival

Considering all individuals which had been trapped at least over 2 trapping sessions ($\geq$11 weeks), we found a lower overall recapture rate in Nabaos (19.3%, n=109) than in Gellap-Ost (31.8%, n=198). Five species were recaptured in Gellap-Ost. These were *T. leucogaster* (37.9%), *G. vallinus* (11.4%), *Aethomys namaquensis* (38.5%), *Elephantulus intufi* (66.7%), *Saccostomus campestris* (33.3%). In Nabaos only *G. vallinus* (22.5%) and *Desmodillus auricularis* (20.0%) were recaptured.

The mean minimum 'survival' rate in weeks (w) shows the longest survival period for *E. intufi* in Gellap-Ost (mean 20.0 w, range 1-64 w, n=9), followed by *A. namaquensis* (mean 9.6 w, range 1-41 w, n=13), *T. leu-*

cogaster (mean 8.5 w, range 1-53 w, n=116), *S. campestris* (mean 4.3 w, range 1-11 w, n=9), *G. vallinus* (mean 3.6 w, range 1-42 w, n=44). In Nabaos *G. vallinus* has 'survived' longer (mean 5.5 w, range 1-44 w, n=80) than in Gellap-Ost, but *D. auricularis* was recorded for only the mean of 3.0 weeks (range 1-10 w, n=11). In total ten individuals had been trapped over a period of >40 weeks : two specimens of *G. vallinus* in Nabaos and one in Gellap-Ost, six specimens of *T. leucogaster* (one female 53 weeks) and one male *E. intufi,* which was still trapped in the last trapping session in Gellap-Ost after a 'survival' of about 64 weeks.

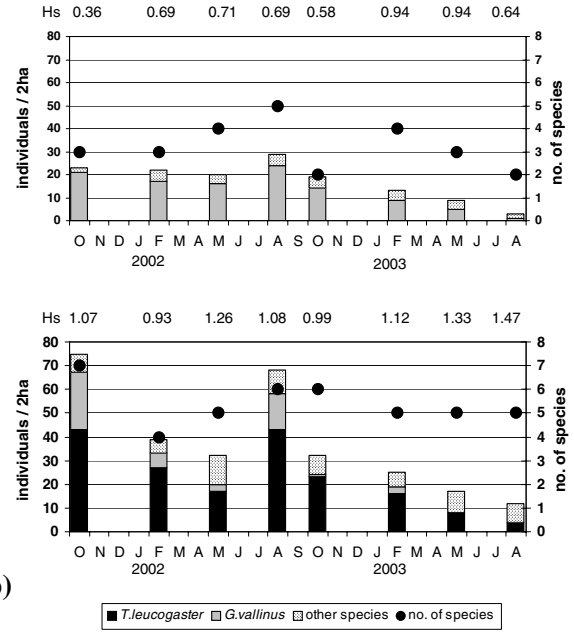

Fig. 2. – a, b : Abundance and diversity of small mammals in neighbouring study sites.
a : Nabaos, **b :** Gellap-Ost. Pictured is the abundance of *G. vallinus* and *T. leucogaster* and other species (pooled), the species number and the Shannon-Wiener-diversity-index for each trapping session.

DISCUSSION

In this study the intensive and uncontrolled grazing by livestock in the communal area had a clear negative impact on species richness, diversity and settlement/survival of small mammals. This suggests that the total loss of ground vegetation cover leads to a reduced food supply (plants, arthropods) and available dew for small mammals. Also disruption of habitat structure, cover and shelter leads to a higher predation risk. Bushes represent areas of high food density and low predation risk (KOTLER, 1984). It is assumed that the decrease of large bushes in the communal area due to the intensive browsing by goats also reduces protection from predation. Burrows in the overgrazed area were found exclusively in bushes, which is probably because of the loss of ground cover, and the direct disturbance by livestock. Intensive and continuous trampling by ungulates is described as a disruptive factor to small mammals (KEESING, 1998; HOFFMANN, 1999; KEESING & CRAWFORD, 2001). Altricial species are much more sensitive to habitat disturbance. Their requirements in the microhabitat in relation to their nest building behaviour are much higher than for precocial species (ZELLER, 2003).

Many small mammal species are able to successfully tolerate and exploit changes in their physical and biological environments (DELANY & HAPPOLD, 1979). Grazing is one example for such an environmental change, which influences stratification of grass, plant species composition and the standing crop biomass of grassland ecosystems (BOWLAND & PERRIN, 1989). The variety and abundance of small mammal communities might be dependent on how grazers have utilized the grassland (GRANT et al., 1982). Overgrazing affects the food (LACK, 1954) and shelter of small mammals (BOWLAND & PERRIN, 1989). The reduction of vegetation cover exposes them to predation (PEARSON, 1971). NYAKO-LARTEY & BAXTER (1995) found that sites under rotation farming, such as the governmental area in Gellap-Ost, and those grazed by cattle, support more rodents than constantly grazed areas and those grazed by sheep. Therefore it is assumed that the habitat differences across the fence-line is not only caused by the intensity of grazing, but also by the differences in feeding behaviour of goats (primarily browsers) and sheep (selective grazers).

In contrast to a study in the Succulent Karoo (JOUBERT & RYAN, 1999), the small mammal composition in the overgrazed area of Nabaos was never just a subset of the species composition encountered in the moderately grazed areas of Gellap-Ost. Nevertheless, a high overlap of occurring species was found in the year round study. The mean species richness recorded in Nabaos was low (3.3), although it is comparable to the species richness (3.8) recorded in the semi-arid Karoo of southern Africa (KERLEY, 1992b) and in different Fynbos habitats in South Africa (BOND et al., 1980; NEL et al., 1980; ELS & KERLEY, 1996). Species richness was much higher in the lightly grazed area of Gellap-Ost (mean : 5.4 species) across the fence-line. The dominance of small mammal communities also varied. The total disappearance of *T. leucogaster* in the overgrazed area and the dominance of *G. vallinus* was conspicuous. The higher 'survival' rate of *G. vallinus* indicates that this xeric adapted species, which is confined to the western sector of the South West Arid Zone and is known to prefer surface sand (DEGRAAFF, 1981; DEMPSTER et al., 1999), found a more suitable habitat in the degraded land than in the grassy area of Gellap-Ost. This confirms the results of a biodiversity study in rangelands of South Africa (FABRICIUS et al., 2003), where the communal grazing area was characterized by xeric adapted reptiles and predatory arthropods, whereas the nature reserve and commercial farms supported more mesic-adapted species. In contrast, *T. leucogaster* is found in a wide range of savannas and open woodlands of southern Africa (DEGRAAFF, 1981; SMITHERS, 1983), where they generally occur in areas with mean annual rainfall of 250 mm and upwards (SKINNER & SMITHERS, 1990). This gerbil occurs in drier areas like the Nama Karoo where it is assumed to depend on an adequate ground vegetation layer not only because of food availability and cover, but also due to dew water availability. CHRISTIAN (1980) assumes that water availability may play an important role in coexistence and resource alloca-

tion in desert rodents. Because *T. leucogaster* were found to be omnivorous (PERRIN & SWANEPOEL, 1987; NEAL, 1991; MONADJEM, 1997) with a high proportion of plant items like seeds, rhizomes and bulblets (DEGRAAFF, 1981), might also explain their exclusive presence in Gellap-Ost.

Several workers in southern Africa have reported correlations between the distributions of individual small mammal species and measured habitat parameters, especially ground cover (BOND et al., 1980; KERLEY, 1992b; MONADJEM, 1997). The quantity of cover is of prime importance to the density and diversity of small mammals, but when cover reaches threshold levels the degree of plant species diversity becomes important (BOWLAND & PERRIN, 1989). A number of studies have shown that small mammal community structure is a function of plant architecture (ROSENZWEIG & WINAKUR, 1969; BOND et al., 1980; KERLEY, 1992b; ELS & KERLEY, 1996). BOND et al. (1980) and ELS & KERLEY (1996) maintain that microhabitat features such as vegetation structure, cover and height, relative humidity, litter depth, and foliage height diversity are directly related to the life form and growth pattern of plant species within a plant community and these factors are important floristic variables affecting small mammal community structure. The mechanism for this relationship is generally thought to be that niche availability (more specifically foraging microhabitat availability) is a function of habitat complexity : a more complex habitat will contain more niches which may be exploited by more species (ROSENZWEIG & WINAKUR, 1969).

Until now small African mammals have not enough considered adequately in both the planning and management of conservation areas, largely due to the difficulty in assessing this group. According to AVENANT (2000), biodiversity of small mammals can be used as an indicator of disturbance in an ecosystem, whereas the domination of an indicator species, low species richness and low diversity are useful tools for indicating disturbance on the primary producer level. An understanding of determinants of small mammal community structure is therefore important for practical development of arid and semi-arid rangeland management guidelines (KERLEY, 1992b). BARNARD et al., (1998) ascertains that the establishment of wildlife conservation in commercial and communal farmlands could improve the current protection status of the Nama Karoo, with rural communities responsible for the ecological management of large areas in habitats otherwise overlooked for conservation.

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REFERENCES

ABRAMSKY, Z. (1988). The role of habitat and productivity in structuring desert rodent communities. *Oikos*, 52 : 107-114.

AVENANT, N.L. (2000). Small mammal community characteristics as indicators of ecological disturbance in Willem Pretorius Nature Reserve, Free State, South Africa. *South African Journal of Wildlife Research*, 30 (1) : 26-33.

BARNARD, P., C.J. BROWN, A.M. JARVIS, A. ROBERTSON & L. VAN ROOYEN (1998). Extending the Namibian protected area network to safeguard hotspots of endemism and diversity. *Biodiversity and Conservation*, 7 : 531-547.

BOND, W., M. FERGUSON & G. FORSYTH (1980). Small mammals and habitat structure along altitudinal gradients in the southern Cape mountains. *South African Journal of Zoology*, 15 : 34-43.

BOWLAND, A.E. & M.R. PERRIN (1989). The effect of overgrazing on small mammals in Umfolozi Game Reserve. *Zeitschrift für Säugetierkunde*, 54 : 251-260.

BRONNER, G. & J. MEESTER (1987). Comparison of methods for estimating rodent numbers. *South African Journal of Wildlife Research*, 17 (2) : 59-63.

CHRISTIAN, D.P. (1980). Vegetative cover, water resources, and microdistributional patterns in a desert rodent community. *Journal of Animal Ecology*, 49 : 807-816.

COWLING, R.M. (1986). A description of the Karoo Biome Project. *South African National Scientific Programmes Report* 122, Pretora.

DeGraaff, G. (1981). *The rodents of Southern Africa.* Durban, Butterworths.

DEAN, W.R.J. & S.J. MILTON (1995). Plant and invertebrate assemblages on old fields in the arid southern Karoo, South Africa. *African Journal Ecology,* 33 : 1-13.

DEAN, W.R.J. & S.J. MILTON (1999). *The Karoo. Ecological patterns and processes.* Cambridge University Press, Cambridge.

DELANY, M.J. (1964). An ecological study of the small mammals in the Queen Elizabeth Park, Uganda. *Revue de Zoologie et de Botanique Africaines*, 70 (1-2) : 129-147.

DELANY, M.J. & D.C.D. HAPPOLD (1979). *Ecology of African mammals.* Longman, London and New York, 434pp.

DEMPSTER, E.R., M.R. PERRIN & C.T. DOWNS (1999). *Gerbillurus vallinus*. *Mammalian Species*, 605 : 1-4.

ELS, L.M. & G.I.H. KERLEY (1996). Biotic and abiotic correlates of small mammal community structure in the Groendal Wilderness Area, Eastern Cape, South Africa. *Koedoe*, 39 (2) : 121-130.

FABRICIUS, C., M. BURGER & P.A.R. HOCKEY (2003). Comparing biodiversity between protected areas and adjacent rangeland in xeric succulent thicket, South Africa : arthropods and reptiles. *Journal of Applied Ecology,* 40 : 392-403.

GRANT, W.E., E.C. BIRNEY, N.R. FRENCH & D.M. SWIFT (1982). Structure and productivity of grassland small mammal communities related to grazing-induced changes in vegetative cover. *Journal of Mammalogy*, 63 : 248-260.

HOFFMAN, M.T., B. COUSINS, T. MEYER, A. PETERSEN & H. HENDRIKS (1999). Historical and contemporary agricultural land use and the deserfication of the Karoo. In : DEAN, W.R.J. & S.J. MILTON (eds), *The Karoo. Ecological patterns and processes*, Cambridge University Press, Cambridge : 257-273.

HOFFMANN, A. (1999). *Habitatnutzung und Populationsdynamik von Kleinsäugern im Grasland des Queen Elizabeth National Park, Uganda.* Dissertation, Technische Universität Braunschweig, (http ://www.biblio.tubs.de/ediss/data/20000114a/20000114a.html).

HOFFMANN, A., K. VOHLAND, P. GIERE & U. ZELLER (2003). Influence of grazing intensity on biodiversity of small mammals and arthropods in the Nama Karoo of southern

Namibia. Abstract. In : *Arid Zone Ecology Forum Conference 2003,* Kathu, South Africa.

HUGHES, J.J., D. WARD & M.R. PERRIN (1994). Predation risk and competition affect habitat selection and activity of Namib desert gerbils. *Ecology,* 75 (5) : 1397-1405.

HUGO, A. (1990). Wiederfangerfolg bei Kleinsäugern mit einer neuen Markierungsmethode. *Zeitschrift für Säugetierkunde*, 55 : 421-424.

JOUBERT, D.F. & P.G. RYAN (1999). Differences in mammal and bird assemblages between commercial and communal rangelands in the Succulent Karoo, South Africa. *Journal of Arid Environment,* 43 : 287-299.

KEESING, F. (1998). Ecology and behavior of the pouched mouse, *Saccostomus mearnsi*, in central Kenya. *Journal Mammalogy,* 79 (3) : 919-931.

KEESING, F. & T. CRAWFORD (2001). Impacts of density and large mammals on space use by the pouched mouse (*Saccostomus mearnsi*) in central Kenya. *Journal of Tropical Ecology,* 17 : 464-472.

KERLEY, G.I.H. (1992a). Small mammal seed consumption in the Karoo, South Africa : further evidence for divergence in desert biotic processes. *Oecologia,* 89 : 471-475.

KERLEY, G.I.H. (1992b). Ecological correlates of small mammal community structure in the semi-arid Karoo, South Africa. *Journal of Zoology, London,* 227 : 17-27.

KOTLER, B.P. (1984). Risk of predation and the structure of desert rodent communities. *Ecology*, 65 : 689-701.

LACK, D. (1954). *The natural regulation of animal numbers.* Oxford, Clarendon Press.

LLOYD, J.W. (1999). Nama Karoo. In : J. KNOBEL (ed), *The magnificent natural heritage of South Africa*, Sunbird Publishing, Cape Town, South Africa : 84-93.

LONDO, G. (1975). De decimale schaal foor vegetatiekundlige opnamen van permanente Kwadraten. *Gorteria*, 7 (7) : 101-106.

LOVEGROVE, B. (1993). *The living deserts of southern Africa.* Fernwood Press, Cape Town.

MENDELSOHN, J., C. ROBERTS & T. ROBERTSON (2002). *Atlas of Namibia. A portrait of the land and its people.* Publisher : Ministry of environment and Tourism of Namibia, Cape Town.

MONADJEM, A. (1997). Habitat preferences and biomasses of small mammals in Swaziland. *African Journal of Ecology*, 35 : 64-72.

MONADJEM, A. (1999). Population dynamics of *Mus minutoides* and *Steatomys pratensis* (Muridae : Rodentia) in a subtropical grassland in Swaziland. *African Journal of Ecology,* 37 : 202-210.

NEAL, B.R. (1991). Seasonal changes in reproduction and diet of the Bushveld gerbil, *Tatera leucogaster* (Muridae : Rodentia), in Zimbabwe. *Zeitschrift für Säugetierkunde,* 56 : 101-111.

NEL, J.A.J., I.L. RAUTENBACH & G.J. BREYTENBACH (1980). Mammals of the Kammanassie Mountains, southern Cape Province. *South African Journal of Zoology*, 15 : 255-261.

NOY-MEIR, I., M. GUTMAN & Y. KAPLAN (1989). Responses of Mediterranean grassland plants to grazing and protection. *Journal of Ecology,* 77 : 290-310.

NYAKO-LARTEY, Q. & R.M. BAXTER (1995). The effects of different grazing regimes on the population dynamics of small mammals in the Eastern Cape. *Transvaal Royal Society of South Africa,* 50 (2) : 143-151.

OLSVIG-WHITTAKER, L.S., P.E. HOSTEN, I. MARCUS & E. SHOCHAT (1993). Influence of grazing on sand field vegetation in the Negev Desert. *Journal of Arid Environment*, 24 : 81-93.

PEARSON, O.P. (1971). Additional measurements of the impact of carnivores on California voles (*Microtus californicus*). *Journal of Mammalogy,* 52 : 41-49.

PERRIN, M.R. & P. SWANEPOEL (1987). Breeding biology of the bushveld gerbil *Tatera leucogaster* in relation to diet, rainfall and life history theory. *South African Journal of Zoology*, 22 (3) : 218-227.

PRICE, M.V. & S.H. JENKINS (1986). Rodents as seed consumers and dispersers. In : MURRAY, D.R. (ed), *Seed dispersal*, Academic Press, Australia : 191-235.

RIVERS-MOORE, N.A. & M.J. SAMWAYS (1996). Game and cattle trampling, and impact of human dwellings on arthropods at a game park boundary. *Biodiversity and Conservation*, 5 : 1545-1556.

ROSENZWEIG, M.L. & J. WINAKUR (1969). Population ecology of desert rodent communities : habitats and environmental complexity. *Ecology*, 50 (4) : 558-572.

ROWE-ROWE, D.T. & T. MEESTER (1982). Habitat preferences and abundance relations of small mammals in Natal Drakensberg. *South African Journal of Zoology*, 17 : 202-209.

SEYMOUR, C.L. & W.R.J. DEAN (1999). Effects of heavy grazing on invertebrate assemblages in the Succulent Karoo, South Africa. *Journal of Arid Environment*, 43 : 267-286.

SKINNER, J.D. & R.H.N. SMITHERS (1990). *The mammals of the southern African subregion*. Pretoria, University of Pretoria.

SMITHERS, R.H.N. (1983). *The mammals of the southern African subregion*. Pretoria, University of Pretoria.

TODD, S.W. & M.T. HOFFMAN (1999). A fence-line contrast reveals effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. *Plant Ecology*, 142 : 169-178.

VENTER, J.M., C. MOCKE & J.M. DE JAGER (1986). Climate. In : CROWLING, R.M., P.W. ROUX & A.J.H. PIETERSE (eds), *The Karoo Biome : a preliminary synthesis. Part 1. Physical Environment.* South African National Scientific Programmes Report 124, Pretoria.

VOHLAND, K., M. UHLIG, E. MARAIS, A. HOFFMANN & U. ZELLER (2005) : Impact of different grazing systems on diversity, abundance and biomass of beetles (Coleoptera), a study from Southern Namibia. *Mitteilungen aus dem Museum für Naturkunde in Berlin, Zoologische Reihe*, 81 (2) : 131-143.

ZELLER, U. (2003). Functional zoodiversity in biomes of southern Africa and its changes by land-use and environment. In : *BIOTA Southern Africa. Towards sustainable use of biodiversity.* Published by University of Hamburg, Botanical Institute and Botanical Garden, Volume I : 231-264.

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Morphological and morphometrical analyses of three cryptic species of *Tatera* Lataste, 1882 (Rodentia : Muridae) from West Africa

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ABSTRACT. Three chromosomally well-differentiated but morphologically similar species of the Gerbilline rodent genus *Tatera* occur in West Africa, namely *T. gambiana*, *T. guineae* and *T. kempi*. In order to find reliable diagnostic characters, morphological and morphometrical analyses were performed on samples of these three species from Mali, the only country where they are known to occur sympatrically. Body measurement comparisons show that *T. guineae* has a longer tail and hindfoot, and *T. gambiana* a shorter ear, relative to the two other species. Skull measurements are less variable between species as only a larger upper tooth row characterizes *T. kempi*, and a shorter tympanic bulla length *T. guineae*. Conversely, geographically distant samples of *T. kempi* from Mali and Chad differ mainly for skull measurements. There is a wide overlap between the ranges of values recorded in the three species. Principal Component and Discriminant Analyses of skull measurements highlight the distinctiveness of *T. guineae*, whose sample is clearly separated from those of *T. kempi* and *T. gambiana*. All these results validate the status of morphologically cryptic species for *T. kempi* and *T. gambiana*, long treated as synonymous. *Tatera guineae* is the most differentiated, but the diagnosis of an individual specimen may prove difficult due to the observed interspecific overlap in all the characters considered.

KEY WORDS : Gerbilline rodents, *Tatera,* skull measurements, multivariate analyses, phenetic similarity.

INTRODUCTION

The Gerbilline rodent genus *Tatera* Lataste, 1882 is widely distributed in all sub-Saharan Africa, occupying a variety of habitats in northern and southern savannas to the margins of the rainforest. MUSSER & CARLETON (1993) recognized twelve species in the genus, the majority of which occur in southern or eastern Africa. Only two of these can be considered as having an exclusive West African range, namely *T. guineae* Thomas, 1910 and *T. kempi* Wroughton, 1906. The first one is characteristic of the Sudan savannas from Senegal, Guinea and Sierra Leone to Burkina Faso and Togo, whereas the second ranges from Sudan to Guinean savannas and from Sierra Leone to eastern Chad and northern Central African Republic. A third species, *T. gambiana* Thomas, 1910, should now be re-evaluated as present in West Africa : Long treated as synonym of *T. kempi*, *T. gambiana* has proven to be a distinct biological species, which main range covers Sahel savannas of Senegal and Mali (MATTHEY & PETTER, 1970; VOLOBOUEV et al., in prep.), with a proposed eastward extension to eastern Niger (DOBIGNY et al., 2002a). On the other hand, the presence of *T. robusta* (Cretzschmar, 1830) in West Africa should still be considered doubtful, as it only relies on one single specimen from Burkina Faso (BATES, 1985).

Tatera taxonomy and systematics has always been a matter of debate. As early as 1906, WROUGHTON highlighted the difficulty in finding and using unambiguously diagnostic morphological characters to recognize species in the genus. This problem has been repetitively mentioned by those who tried to organize the variability observed in *Tatera* into a coherent taxonomic arrangement (PIRLOT, 1955; DAVIS, 1966; ROSEVEAR, 1969; MATTHEY & PETTER, 1970; TRANIER, 1974; BATES, 1985 & 1988). Since the first karyotypic data obtained by MATTHEY (1954), cytogenetics has proven to be of great help in species identification, and chromosome data have accumulated for this genus (see QUMSIYEH & SCHLITTER, 1991 for a review until 1990; COLANGELO et al., 2001; VOLOBOUEV et al., in prep.). As for West African species, there is now a general agreement on karyotypic characteristics of *T. gambiana* (2n=52), *T. guineae* (2n=50) and *T. kempi* (2n=48; COLANGELO et al., 2001; VOLOBOUEV et al., in prep.).

These three species have been found in southern Mali, which as such represents a unique crossroads for this genus in West Africa. Based on series of karyotyped and therefore unambiguously determined specimens, we try here to find morphological and/or morphometrical characteristics enabling their determination in the field or from museum specimens. Interspecific variability of the characters used was assessed in *T. kempi* through the comparative study with a sample from Chad, i.e. the eastern extreme of the species range.

MATERIALS AND METHODS

All the specimens used in this study were karyotyped following standard procedures (see GRANJON & DOBIGNY, 2003 for instance). They are currently deposited as skin and skull specimens in the small mammal collection of the Institut de Recherche pour le Dévelopement, Bamako and will ultimately be housed at the Museum National d'Histoire Naturelle, Paris. The samples from Mali are as follows : 7 *T. kempi* (M177, M178, M179, M180, M196, M197, M198) from Founé (12°50'N - 4°42'W); 15 *T. gambiana* from various localities of west (Sekokoto : 13°31'N – 10°45'W, N=1 : M4178; Maréna : 14°38'N - 10°36'W, N=2 : M4183, M4190) and central south (Katibougou : 12°30'N – 8°6'W, N=1 : M4412; Samanko : 12°32'N – 8°5'W, N=7 : M4909, M4912, M4916, M4918, M4954, M4955, M4978; Samaya : 12°34'N – 8°4'W, N=4 : M194, M195, M199, M202); and 24 *T. guineae* from various localities along the Guinean border, mainly in the Mts Mandingues region (Kolobo : 13°15'N – 11°31'W, N=1 : M4170; Gainsoa : 12°27'N – 10°15'W, N=1 : M4723; Balamansala : 12°11'N – 8°48'W, N=8 : M4670, M4694, M4709, M4753, M4796, M4858, M4864, M4902; Kigniélendo : 12°20'N – 8°32'W, N=1 : M4664; Kangaba : 11°58'N – 8°25'W, N=1 : M188), in the central south (Niamana : 13°01'N – 8°14'W, N=4 : M4015, M4019, M4093, M4111; Kalifabougou : 12°57'N – 8°11'W, N=7 : M4037, M4044, M4048, M4099, M4104, M4107, M4114) and near the border with Burkina Faso in the south east (Mamouroubougou : 11°12'N – 5°29'W, N=1 : M4879). Additionnally, 23 specimens of *T. kempi* from the Zakouma National Park in south eastern Chad (10°41'N – 19°29'E) were included (I16, H2, O2, O5, O9, O26, O27, O28, O29, O38, O45, O46, P'3, Q10, Q17, Q19, Q20, Q27, Q43, R6, R7, R8, R13). All specimens were adult, most (60 of 67) belonging to age classes 2 or 3 following the 4-class system of BATES (1985) based on dental wear.

The following classical body measurements were taken, to the nearest gram or millimetre : Weight (Wt), head and body length (HB), tail length (T), ear length (E) and hindfoot lenth, excluding claw (HF). A selection of 11 skull measurements was made, based on their presumptive usefulness as revealed by previous studies, especially those of BATES (1985, 1988) and COLANGELO et al. (2001) : Greatest length of skull (GLS), condylobasal length (CBL), greatest width of skull (GWS), breadth of braincase (BB), interorbital constriction (IC), rostral width (RW), rostral length (RL), trans molar width (TMW), tympanic bulla length (TBL), mandible length (ML) and upper toothrow length (UTR). They were taken as described in BATES (1988), to the nearest 0.1mm. Skulls were examined for possible diagnostic characters. Special attention was paid to the first lower molar, the first lamina of which was characterized following the patterns illustrated in BATES (1988).

Measurements were compared by means of student t tests. Eight skull measurements were used to run Principal Component (PCA) and Discriminant (DA) analyses, using SYSTAT 8.0 (1998). GLS, RL and ML were abandoned because they could not be taken in a number of specimens and/or they were highly correlated with other characters. PCA was run using the covariance matrix on log-transformed data, whereas DA gave better results based on non-transformed data.

RESULTS

The mean and standard deviation values, as well as ranges of all measurements taken on the 4 *Tatera* samples, are summarized in Table 1. Distributions of individual dental wear data were compared between samples, prior to other statistical tests : None of the differences observed was found significant via non parametric Wilcoxon tests (P=0.083 between *T. kempi* from Mali and from Chad, P=0.194 between *T. kempi* and *T. gambiana* from Mali, P=0.059 between *T. kempi* and *T. guineae* from Mali, and P=0.924 between *T. gambiana* and *T. guineae*). Based on the hypothesis that age is one of the important determinants of dental wear in rodents, this suggests that the samples compared can be considered of similar age, which makes the following comparisons more relevant. Sexual dimorphism was tested for all body and skull measurements in the three largest samples (*T. kempi* from Chad, *T. gambiana* and *T. guineae* from Mali), using Mann-Whitney U test. Significant differences ($0.01<P<0.05$) were found in only 5 (of 48) instances, males being in all cases larger : Wt, HB and T in *T. kempi* from Chad, Wt and IC in *T. gambiana* from Mali. According to these results, sexual dimorphism was considered negligible in the samples here used and males and females were pooled in subsequent analyses.

Given the relatively small sample sizes, the differences recorded by student t tests were conservatively quoted as significant only when $P<0.01$. *T. gambiana* and *T. kempi* from Mali are the two samples showing the fewer number of differences (n=3), whereas *T. gambiana* and *T. guineae* on the one hand, *T. kempi* from Mali and *T. kempi* from Chad on the other hand, display significant differences for 7 measurements each. Regarding body measurements in the Malian samples, *T. guineae* is characterized by a longer tail and longer hindfoot than both *T. gambiana* and *T. kempi*, the latter sharing a long ear with *T. guineae* relative to *T. gambiana*. Skull measurements do not show many significant differences between species. The main one concerns UTR, significantly longer in *T. kempi* than in the two other species, and TBL, significantly shorter in *T. guineae* than in the two other species. Overlap between ranges of values is the rule, with the exception of tail length in the sample of *T. guineae* when compared with the samples of the two other species from Mali. Differences between the two geographically distinct samples of *T. kempi* often concern measurements that are not significantly variable between species in Malian samples, and are mainly skull ones.

The distribution of individuals of the four study samples according to the morphology of their first lower molar first lamina is summarized in Table 2. Most of the *T. gambiana* and *T. kempi* specimens are characterized by a M_1 first lamina opening posteriorly, *vs* only half of the *T. guineae* specimens, the other half having their first lamina divided into 2 islands.

TABLE 1

Body and skull measurements (in mm) of 4 samples of *Tatera*, and associated student t tests results (*p<0.01; **p<0.001; ***p<0.0001)

		Wt	HB	TL	H	E	GLS	CBL	GWS	BB	IC	RW	RL	TMW	TBL	ML	UTR
	N	15	15	11	15	15	12	14	12	15	15	14	11	13	15	15	14
T. gambiana Mali	Mean	114.47	153.33	144.82	30.83	19.70	38.20	34.63	19.10	15.70	6.35	5.27	13.14	8.16	10.17	24.29	5.79
	St. Deviation	30.208	13.819	8.542	1.397	1.207	1.523	1.388	0.998	0.400	0.302	0.289	0.905	0.312	0.415	1.413	0.164
	Range	78-180	139-188	128-160	29-35	18-22	36.5-41.2	31.8-36.7	17.5-20.7	15.1-16.5	6.0-7.0	4.9-5.9	11.8-14.7	7.8-8.7	9.2-10.7	20.9-26.4	5.4-6
	N	24	24	5	23	24	20	24	19	24	24	24	19	24	24	20	23
T. guineae Mali	Mean	87.13	143.00	173.20	34.87	21.21	37.85	33.87	18.56	15.50	6.55	5.56	14.28	7.94	9.68	22.93	5.65
	St. Deviation	22.046	12.857	6.496	1.236	0.871	1.864	1.737	1.175	0.434	0.308	0.399	1.122	0.395	0.593	1.215	0.178
	Range	50-136	116-164	163-179	32-37	20-23.5	33.5-40.6	30.4-36.4	16.7-21.2	14.9-16.3	6-7.3	4.9-6.9	11.5-15.8	7.1-8.5	9-11.6	20.3-25.6	5.3-5.9
	N	7	7	5	7	7	5	6	6	6	7	7	6	6	6	6	6
T. kempi Mali	Mean	77.71	138.14	138.20	32.57	21.86	39.22	35.90	19.83	15.92	6.39	5.33	13.68	8.25	10.67	23.95	6.03
	St. Deviation	12.134	12.522	12.696	1.512	1.069	0.712	0.626	0.680	0.392	0.344	0.111	0.325	0.226	0.216	0.243	0.175
	Range	56-90	120-155	120-150	31-34	20-23	38.1-40	35-36.7	18.6-20.3	15.4-16.4	5.9-6.7	5.1-5.4	13.3-14.2	8-8.5	10.4-10.9	23.6-24.3	5.7-6.2
	N	23	23	19	23	23	19	23	22	23	23	23	17	23	23	21	23
T. kempi Chad	Mean	71.96	138.96	149.26	31.87	20.07	36.79	34.00	18.37	15.65	6.32	5.03	12.59	7.73	10.50	23.44	5.89
	St. Deviation	12.517	9.883	8.937	1.245	1.237	1.422	1.331	0.672	0.413	0.223	0.260	0.604	0.268	0.389	0.931	0.183
	Range	51-101	114-159	127-170	28-33.5	17-21.5	33.1-40	30.4-37.2	16.9-20.5	14.7-16.4	6-6.9	4.5-5.7	11.5-14.1	7.3-8.6	9.6-11.2	21.1-25.8	5.3-6.1
gambiana vs guineae		*	NS	***	***	***	NS	NS	NS	NS	NS	NS	*	NS	*	*	NS
gambiana vs kempi		*	NS	NS	NS	**	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	*
guineae vs kempi		NS	NS	**	**	NS	NS	*	NS	NS	NS	NS	NS	NS	**	NS	***
kempi Mali *vs kempi* Chad		NS	NS	NS	NS	*	*	*	***	NS	NS	*	**	**	NS	NS	NS

TABLE 2

Morphology of the first lower molar first lamina (see Bates, 1988 for an illustration)

	T. gambiana	*T. guineae*	*T. kempi* (Mali)	*T. kempi* (Chad)
1st lamina open posteriorly	12	8	5	22
1st lamina open anteriorly	0	0	0	0
1st lamina divided into 2 islands	1	8	1	0
Other	0	0	1	1

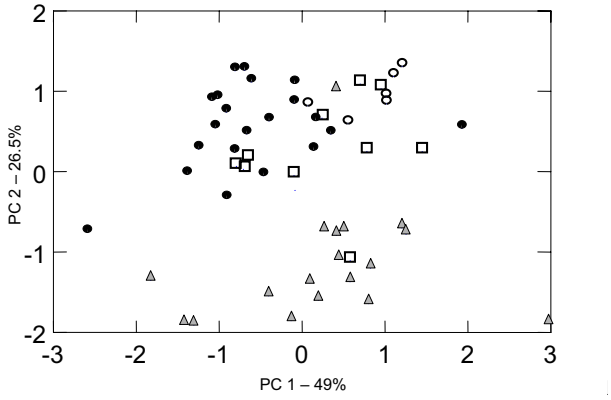

Fig. 1. – Scatter plot of the first two Principal Components (F1 x F2) of the PCA run on 8 log-transformed skull measurements of the four samples of *Tatera* from Mali (*T. gambiana* - squares, *T. guineae* - triangles & *T. kempi* – open circles) and Chad (*T. kempi* – black circles).

The scatter plot of the first two principal components is represented in Fig. 1 (representing more than 75% of the total variance of the original matrix). All the characters correlate positively with PC 1, which thus represents an overall size axis. The main loadings on this axis are from RW, GWS, CBL, TMW and IC. The dispersion of individuals of the four study samples along this factor matches quite well the age-related differences in size observed within each sample. Most of the inter-samples differentiation occurs along PC 2, which mainly separates *T. guineae* from the other three samples. The variables which contribute the most to this discrimination are TBL (positive loading) and RW (negative loading). Overlap between the two *T. kempi* and the *T. gambiana* samples is important, and stay so along PC 3 or 4 (not shown).

The scatter plot of the first two discriminant vectors represents more than 95% of the total dispersion among the study samples (Fig. 2). The associated classification matrix indicates that all *T. guineae* (14/14) and *T. kempi* from Mali (6/6) are correctly classified by the analysis, *vs* only 9 of 10 *T. gambiana* and 19 of 21 *T. kempi* from Chad, yielding an overall value of 94% of well-classified individuals.

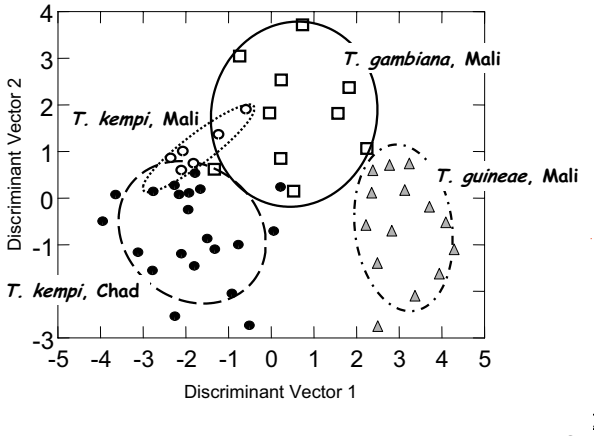

Fig. 2. – Scatter plot of the first two Discriminant Vectors from the DA of 8 raw skull measurements of the four samples of *Tatera* from Mali (*T. gambiana*, *T. guineae* & *T. kempi*) and Chad (*T. kempi*). Confidence ellipses drawn using "Sample" option with *P*=0.683.

The hierarchical classification (Single Linkage Method) based on Mahalanobis distances between group means (Fig. 3) shows that the two *T. kempi* samples are phenetically the most similar, *T. guineae* being the most divergent. When both *T. kempi* samples are pooled in DA, the overall percentage of well-classified individuals remains 94%, (2 *T. kempi* and 1 *T. gambiana* misclassified). When only samples from Mali are considered, this value raises to 97%, only one *T. gambiana* being mistaken for a *T. kempi*.

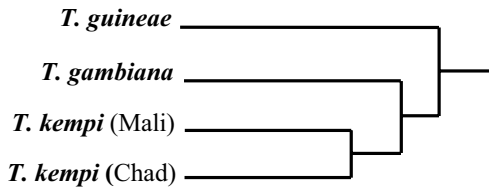

Fig. 3. – Hierarchical classification (single linkage method) based on Mahalanobis distances between the four samples of *Tatera* studied in DA (cf Fig. 2).

DISCUSSION

The validity of the various characters that have been used to distinguishing between species and species groups in *Tatera* has been critically discussed by DAVIS (1966) and ROSEVEAR (1969). DAVIS (1966) distinguished an *afra* and a *robusta* group based on a series of characters showing a relatively large degree of overlap. Among the 3 species studied here, *T. kempi* and *T. gambiana* are considered to belong to the *afra* group, and *T. guineae* to the *robusta* one. As a matter of fact, the general coloration of *T. kempi* and *T. gambiana* is usually quite dull, their pelage is rather harsh and their tail shorter or subequal than head and body, without a densely haired terminal pencil while the pelage of *T. guineae* is more silky with a brighter coloration, and its tail is usually much longer than head and body, with a marked terminal pencil of

hairs. These tail characteristics appear to be reliable whenever the tail is complete, while pelage aspect is more subject to individual variation.

Similarly, skull characters are difficult to associate to one or another species. No one has been found to unambiguously characterize any of the three species here studied. Even the morphology of the zygomatic plate, said to project less forward in *T. guineae* than in other West African species by ROSEVEAR (1969), can be of ambiguous interpretation. The morphology of the M_1 first lamina used by BATES (1988) to distinguish between *T. valida valida* and *T. valida kempi* also diplayed variability within each sample. However, it proved to be less variable in both the *T. kempi* samples studied here than in the one, mainly from Benin, analysed by COLANGELO et al. (2001). Here, and as in *T. gambiana*, the first lamina opens posteriorly in the vast majority of individuals, as supposed to be the rule in *T. kempi* according to BATES (1988).

Measurements give useful information on species characteristics, but they can hardly be used on an individual basis to identify a given specimen unambiguously, as the range of values overlap widely in most cases. The same was observed by BATES (1985) in his comparative analysis of cryptic species from East Africa, namely *T. robusta*, *T. nigricauda* (Peters, 1878) and *T. phillipsi* (de Winton, 1898). This casts doubt on the absolute diagnostic value of some of the criteria proposed by ROSEVEAR (1969) and resumed by MATTHEY & PETTER (1970) to distinguish between *Tatera* species in West and Central Africa (e.g. molar row length or bullae length, but see hereunder). As said above, tail length is especially helpful in discriminating *T. guineae* from the other species, as is hind foot length. Combining these two measurements, in bivariate plots, clearly separate *T. guineae* from the two other species (not shown here due to scarcity of data on tail length). As for skull measurements, the short bullae of *T. guineae* and the long molar row of *T. kempi* were already used by ROSEVEAR (1969) in his determination key for West African species of *Tatera*. The large maxillary tooth row in *T. kempi* was also mentioned by COLANGELO et al. (2001) in their sample from Benin, when compared with data on *T. nigrita* WROUGHTON, 1906 (= *T. valida* Bocage, 1890 in MUSSER & CARLETON, 1993) from Chad published by TRANIER (1974). However, comparing skull measurement data of *T. kempi* from Mali or Chad with those on *T. kempi* from Benin presented by COLANGELO et al. (2001) shows that the latter are systematically larger. This trend is not associated with an older mean age of the sample from Benin, as the differences of dental wear distribution between this sample and the two *T. kempi* ones of our study are not significant (Wilcoxon non parametric test, P=0.339 with Malian sample, P=0.837 with Chadian sample). Conversely, it could be linked with the way in which the measurements were taken (experimental bias), but may also illustrate a true geographical variation. The latter interpretation is reinforced by the differences observed here between the samples from Chad and Mali. It has also to be underlined that none of the variables used in bivariate representations by BATES (1985, 1988) to separate between East African species proved to be of use here (GLS vs RW or BB; RW vs RL), showing again the great similarity between the skulls of the samples under study.

Multivariate analyses confirmed the distinctiveness of *T. guineae*, which even appeared well distinct in PCA ordination. Conversely, *T. gambiana* and *T. kempi* still show some overlap in the distribution of their individuals in the DA space. This confirms the validity for West African species of the distinction between the *afra* and *robusta* groups made by DAVIS (1966). Within the species of the *afra* group, the percentage of misclassified individuals between *T. kempi* and *T. gambiana* was weak, which makes it possible to envisage successful assignation of unknown individuals with rather great confidence based on this kind of analyses. For that purpose, sample sizes of unambiguously determined individuals should be enlarged, so that age-related (and possibly sex-related) variation can be taken into account more precisely. But even with such precautions, one should keep in mind that this kind of use should be restrained to geographically well-defined regions : Geographical variation, here illustrated between samples of *T. kempi* from Mali and Chad, is always important and counfounding in such groups of cryptic species, a qualifier that certainly applies to these West African *Tatera*, as it does for East African ones (BATES, 1985) or for the related genus *Taterillus* Thomas, 1910 (DOBIGNY et al., 2002b).

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REFERENCES

BATES, P.J.J. (1985). Studies of gerbils of genus *Tatera* : The specific distinction of *Tatera robusta* (Cretzschmar, 1826), *Tatera nigricauda* (Peters, 1878) and *Tatera phillipsi* (De Winton, 1989). *Mammalia*, 49 : 37-52.

BATES, P.J.J. (1988). Systematics and zoogeography of *Tatera* (Rodentia : Gerbillinae) of north-east Africa and Asia. *Bonn. Zool. Beitr.*, 39 : 265-303.

COLANGELO, P., M.V. CIVITELLI & E. CAPANNA (2001). Morphology and chromosomes of *Tatera* Lataste, 1882 (Rodentia Muridae Gerbillinae) in West Africa. *Tropical Zoology*, 14 : 243-253.

DAVIS, D.H.S. (1966). Contribution to the revision of the genus *Tatera* in Africa. *Ann. Mus. Roy. Afr. Centr. Zool.*, 144 : 49-65.

DOBIGNY, G., A. NOMAO & J.C. GAUTUN (2002a). A cytotaxonomic survey of Rodents from Niger : implications for systematics, biodiversity and biogeography. *Mammalia*, 66 : 495-523.

DOBIGNY, G., M. BAYLAC & C. DENYS (2002b). Geometric morphometrics, neural networks and diagnosis of sibling *Taterillus* species. *Biological Journal of the Linnean Society*, 77 : 319-327.

GRANJON, L. & G. DOBIGNY (2003). The importance of cytotaxonomy in understanding the biogeography of African rodents : Lake Chad murids as an example. *Mammal Review*, 33 : 77-91.

MATTHEY, R. (1954). Nouvelles recherches sur les chromosomes des Muridae. *Caryologia*, 6 : 1-44.

MATTHEY, R. & F. PETTER (1970). Etude cytogénétique et taxonomique de 40 *Tatera* et *Taterillus* provenant de Haute-Volta et de République Centrafricaine (Rongeurs, Gerbillidae). *Mammalia*, 34 : 585-597.

MUSSER, G. & M.D. CARLETON (1993). Family Muridae. In : WILSON, D.E. & D.M. REEDER (eds), *Mammal species of the world : a taxonomic and geographic reference*, Smithsonian Inst. Press, Washington : 501-755.

PIRLOT, P.L. (1955). Variabilité intra-générique chez un rongeur africain (*Tatera* Lataste). *Ann. Mus. Congo, Tervuren, Zool*., 39 : 9-66.

QUMSIYEH, M.B. & D.A. SCHLITTER (1991). Cytogenetic data on the rodent family Gerbillidae. *Occ. Papers Mus. Texas Tech Univ.*, 144 : 1-20.

ROSEVEAR, D.R. (1969). *The rodents of West Africa*. Trustees of the British Museum (Natural History), London, 604p.

SYSTAT (1998). SYSTAT for Windows, Version 8.0, SPSS Inc., Chicago.

TRANIER, M. (1974). Dimorphisme chromosomique dans une population de *Tatera* du Sud du Tchad (Rongeurs, Gerbillidés). *Mammalia*, 38 : 224-233.

WROUGHTON, R.C. (1906). Notes on the genus *Tatera* with descriptions of new species. *Ann. Mag. Nat. Hist*., 7 (17) : 474-499.

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Survival and roost-site selection in the African bat *Nycteris thebaica* (Chiroptera : Nycteridae) in Swaziland

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ABSTRACT. Survival and mortality of African bats is poorly known. A banding study of a population of *Nycteris thebaica*, roosting in 15 road culverts in north-eastern Swaziland, was initiated in 1998. Since then, a total of 799 bats have been banded including five cohorts of same-aged individuals of known age. Cohort life-tables and survivorship curves were calculated using these data. For both males and females, survivorship was low in the first year, but increased thereafter. Approximately 15% of females and 10% of males banded as juveniles in 1998 and 1999 survived to three years of age. Of female bats banded as adults in July 1998 (n = 39), 23% had survived to January 2003 (4.5 years). The corresponding value for males (n = 6) was zero. Of 28 male bats banded in 1998, only one (4%) was recaptured after four years. Female values probably reflect true survival and mortality, whereas, dispersal and movement complicate the values for males. Female *Nycteris thebaica* did not randomly select roosting sites. The 15 culverts were occupied by six discrete groups of female bats. The presence of male bats at the study site was irregular, with movements of 9 km having been recorded by one particular individual.

KEY WORDS : *Nycteris thebaica*, survival, roost selection, Africa.

INTRODUCTION

The ecologies and life histories of African bats are relatively poorly known. For many species, even basic distributional information is highly fragmented and far from complete. To date, most bat studies in Africa have focused on distribution, taxonomy, reproduction and to a lesser extent on diet, domiciles and echolocation. Limited information is available on other biological aspects of African bats including longevity, survival and the behavioural and ecological aspects of roost-site selection. Some notable exceptions are VAN DER MERWE (1989) who showed that *Miniopterus schreibersii natalensis* (A. Smith, 1834) could survive up to 13 years in South Africa, LAVAL & LAVAL (1977), O'SHEA (1980) and HAPPOLD & HAPPOLD (1990, 1996) who investigate roost-site selection and other aspects of social behaviour in *Pipistrellus nanus* (Peters, 1852). Other species of Sub-Saharan Africa microchiropterans whose roosting behaviour have been studied include *Myotis bocagii* (Peters, 1870) (BROSSET, 1976), *Coleura afra* (Peters, 1852) (MCWILLIAM, 1987), *Lavia frons* (E. Geoffroy, 1810) (WICKER & UHRIG, 1969) and *Tadarida pumila* (Cretzschmar, 1830-1831) (MCWILLIAM, 1987).

The microchiropteran bat *Nycteris thebaica* E. Geoffroy, 1818 is widespread in Africa, and tolerates a wide range of environmental conditions (SMITHERS, 1983), roosting in caves, mine adits and various other hollow sites (CHURCHILL et al., 1997; TAYLOR, 1998; TAYLOR, 2000). In Swaziland, it regularly roosts in road culverts where adult females significantly outnumber adult males (MONADJEM, 1998; MONADJEM, 2001). Females are present in significant numbers throughout the year, but it is not known whether these individuals regularly move between culverts or use one or a few culverts exclusively.

Nycteris thebaica often uses different day and night roosts (TAYLOR, 1998). Night roosts are generally associated with feeding (BOWIE et al., 1999; SEAMARK & BOGDANOWICZ, 2002), while day roosts appear to function as resting sites.

The main objectives of this study were to : 1) determine the age-specific survival of *Nycteris thebaica* in Swaziland, and 2) investigate daytime roost-site selection in this species.

METHODS

This study was conducted at Mlawula Nature Reserve (26E 11'S; 31E 59'E, 160 m above sea level) in the lowveld of northeastern Swaziland. Mlawula Nature Reserve typically experiences hot, wet summers (October to March) and cool, dry winters (May to August). Mean annual rainfall is approximately 500-600 mm, but rainfall can vary dramatically between years.

The road leading to the main entrance of the reserve is tarred and is situated within the reserve. It is approximately 3 km in length and passing beneath this road are 15 culverts 60-100 cm wide and up to 50 m long. *Nycteris thebaica* has been known to be using these culverts as daytime roosts for, at least, the past 15 years (MONADJEM, 2001). The bats roosting within these 15 culverts formed the basis of this study. A small number of *Nycteris thebaica* was also captured in culverts passing under the railway track within 10 km of the main study area. Bats were captured in the culverts by pushing a "shield" (a piece of chipboard with the diameter of the culvert) through the

culvert into a large sweep net placed over the entrance. The other end of the culvert was blocked to prevent bats that had manoeuvred past the shield from leaving the culvert. The process was repeated until all bats had been captured. In the first year of study this technique was not fully developed and occasionally many bats escaped. From August 1999, however, very few bats escaped. All captured bats were sexed, aged and were fitted with metal bat-bands which were attached around the forearm. Three age classes were identified : juveniles, sub-adults and adults. Juveniles were defined as being dependent on their parents and were easily identified by size and pelage, which was greyer than that of the adults. Sub-adults were identifiable by pelage colour (which was still greyer than that of the adults) only in February and probably March, and represented individuals born in the previous breeding season i.e. November. By July the bats were more than 7 months of age, and could no longer be differentiated from older bats (MONADJEM, 2001).

Culverts were surveyed in July, October and December 1998. From August 1999, culverts were surveyed four times per year in July/August, October, December/January and February. In 1998, only two culverts were surveyed. From August 1999 all 15 culverts were surveyed, and all bats captured, during each survey.

Cluster analysis, conducted by the computer program "Primer" (CLARKE & GORLEY, 2001), was used to identify clusters of roost sites based on the adult males and females utilizing them. Dendrograms were generated based on Bray-Curtis similarities computed on the number of times each bat was recorded roosting in each culvert. Counts were square-rooted so as to down-weight the contributions of a few individuals recorded many times in relation to individuals recorded just once.

RESULTS

A total of 799 bats have been banded since 1998 and there have been 1835 recaptures. Of these, 380 were banded as juveniles. Numbers of juveniles banded varied between years, but the ratio of juveniles to adult females did not differ significantly between the years ($\chi^2 = 3.930$, degrees of freedom = 4, $P > 0.05$; Table 1). Between 1998 and the end of 2000, adults formed a significant proportion of new bats banded. From 2001 onwards, however, a decreasing number of bats were first captured as adults (Fig. 1). Juveniles comprised only 45% of all new bats in the first three years of the study, but 57% in 2001 and 81% in 2002.

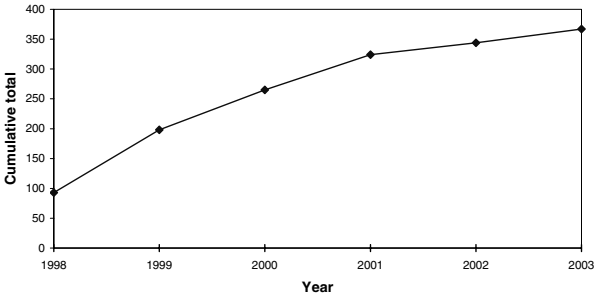

Fig. 1. – Cumulative total number of new (i.e. unbanded) adult *Nycteris thebaica* cap-

The sex ratio of juveniles did not deviate significantly from parity. In total, 196 female and 181 male juveniles were banded, with three unsexed individuals. Juvenile sex ratio also did not differ significantly between years ($\div^2 = 4.359$, degrees of freedom = 4, $P > 0.05$; Table 1).

TABLE 1

Numbers of juveniles banded per year, including juvenile sex ratio and productivity of adult females. Totals do not add up for the years 1999, 2001 and 2002 as single unsexed individuals were banded in these years.

Year	Number of juveniles banded			Juvenile sex ratio (male/ female)	Offspring per adult female
	Male	Female	Total		
1998	13	6	19	2.0	0.8
1999	39	47	87	0.8	1.1
2000	53	55	108	1.0	1.0
2001	36	41	78	0.9	0.8
2002	40	47	88	0.8	0.8

Survivorship curves were similar in shape for male and female bats banded as juveniles (Fig. 2). However, male survival was lower than that of females. Juvenile survival was lowest in the first six months, thereafter levelling off and remaining similar throughout adult life. Approximately 15% of females and 10% of males banded as juveniles in 1998 and 1999 survived to three years of age. Of female bats banded as adults in July 1998 (n = 39), 23% had survived to January 2003 (4.5 years). The corresponding value for males (n = 6) was zero. Of 28 male bats banded in 1998, only one (4%) was recaptured after four years. Adult bats captured in 1998 would have been born at the latest in November 1997 making them over five years old when recaptured in 2003.

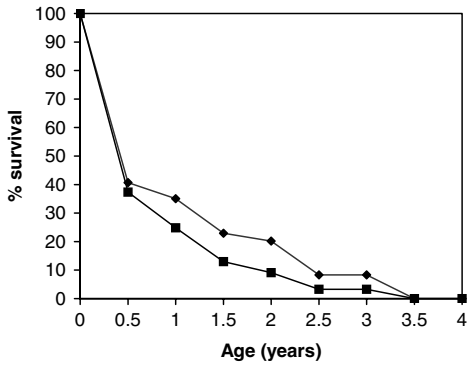

Fig. 2. – Survivorship curves for male (square) and female (diamond) *Nycteris thebaica* banded as juveniles.

Approximately a third of all juvenile females survived to one year, while only a quarter of juvenile males survived to the same age (Table 2). However, this was not statistically different ($\chi^2 = 1.301$, degrees of freedom = 1, $P > 0.05$). Survival to one year varied between years (males : $\chi^2 = 21.416$, degrees of freedom = 3, $P < 0.05$; females : $\chi^2 = 9.582$, degrees of freedom = 3, $P < 0.05$), with highest survival of females and males recorded in 1998 and 1999, respectively. Survival was lowest for both sexes in 2001.

TABLE 2

Minimum estimates of first year survival of juvenile *Nycteris thebaica*.

Year	Proportion juvenile females surviving (n)	Proportion juvenile males surviving (n)	Total number surviving	Overall proportion
1998	0.50	0.15	5	0.26
1999	0.38	0.54	38	0.44
2000	0.38	0.19	31	0.29
2001	0.15	0.11	10	0.13
Mean ± SE	0.35 ± 0.07	0.25 ± 0.10		0.28 ± 0.06

Bats were recorded roosting in 13 of the 15 culverts, with some culverts regularly supporting large numbers of bats (Table 3). Adult bats did not utilize these day roost sites randomly. Adult females tended to be captured in the same culvert on consecutive surveys, occasionally being recorded in neighbouring culverts. This is illustrated in the cluster analysis presented in Fig. 3. Neighbouring roosts cluster together in this analysis, demonstrating similarity in the female "community" using these roosts. Six major groupings are apparent, suggesting that females live in groups whose adult female composition is fairly stable (Fig. 3a). A similar pattern is shown by male bats, however, neighbouring roosts do not necessarily cluster together (Fig. 3b), suggesting greater movement between nonadjacent culverts for males than for females.

Fig 3 (a)

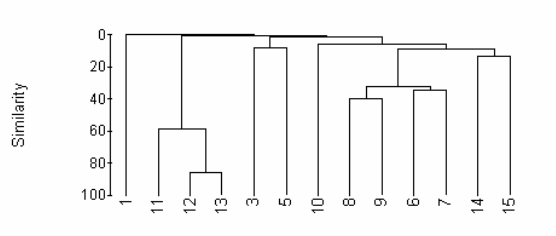

Fig 3 (b)

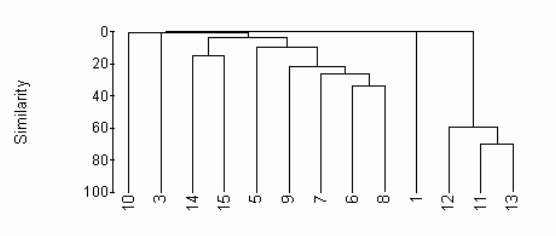

Fig. 3. – Cluster analysis showing relationships between culverts based on : a) female and b) male *Nycteris thebaica* roosting in the 15 culverts. The numbers refer to culvert numbers presented in Table 3. The six female groups are as follows : group 1 (culvert 1), group 2 (culverts 3 & 5), group 3 (culverts 6, 7, 8 & 9), group 4 (culvert 10), group 5 (culverts 11, 12 & 13), group 6 (culverts 14 & 15).

TABLE 3

Total number, mean number and adult sex ratio (male :female) of bats recorded in each of the 15 culverts, and rates of occupancy. Culverts 6 and 7 were surveyed 19 times each; all remaining roosts were surveyed 16 times (see Methods).

	Culverts														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Proportion of visits occupied.	0.50	0	0.31	0	0.25	0.26	0.42	0.69	0.81	0.25	0.38	0.31	0.31	0.31	0.88
No. of bats.	48	0	65	0	92	216	210	345	373	33	19	13	16	41	364
No. of bats/visit when occupied.	6	-	13	-	23	43	26	32	29	8	3	3	3	8	27
Adult sex ratio.	0.21	-	0.45	-	0.62	0.18	0.14	0.24	0.23	0.18	0.20	0.25	0.83	0.44	0.23

DISCUSSION

The proportion of new (unbanded) adults decreased over the duration of the study, demonstrating that levels of immigration into the study population are low. This suggests that emigration from the study area may be correspondingly low. Similar low levels of dispersal have been reported for other species of microchiropteran bats (O'DONNELL, 2000; SWIFT, 1998). Thus, the recapture rates of banded bats in this study are thought to reflect survival.

Juvenile sex ratio did not deviate from parity. The sex ratio of the 1998 cohort, though biased toward males, was not statistically significant and probably a result of the small sample size, which in turn was due to the fact that only two out of 15 culverts were surveyed in that year. The female-biased adult sex ratio (MONADJEM, 2001), therefore, must be a result of differences in survival and/or dispersal after weaning. Rates of recapture were higher for females than for males. Whether this is due to greater mortality among males or whether a greater proportion of males disperse from natal roost sites is not known. However, the sex ratio of immigrant (unbanded) bats is not different from that of resident (banded) bats (male :female = 0.41 and 0.47, respectively; $\chi^2 = 0.830$, $P > 0.05$), suggesting that the skewed sex ratio may be due to differential survival rates. Greater female survival has

also been reported for *Chalinolobus tuberculatus* (O'DONNELL, 2002) and *Plecotus auritus* (SWIFT, 1998).

Nycteris thebaica is long-lived with relatively high rates of adult survival. More than a fifth of the adult females captured at the beginning of the study survived at least five years. Comparable results for other species of African bats are severely limited. *Miniopterus schreibersii natalensis* has been shown to survive at least 13 years but survival rates were not estimated (VAN DER MERWE, 1989).

Mortality rates, in contrast, were high in the first year after birth and varied between years. The high survival rate of females born in 1998 may have been due to the small number of juveniles sampled in that year. The apparently low survival of males and females born in 2001 is probably an artifact of methodology. Survival to one year was indicated not only by recaptures after exactly one year, but also subsequent recapture of individuals one-and-a-half, two or more years later. Thus an individual recaptured for the first time after two years, would have been registered as being alive after one year, even though it was not captured at that time. For this reason, the survival values for this cohort may increase with subsequent sampling. Excluding 2001 values, average first year survival was 0.42 for females and 0.29 for males. This is slightly lower compared with estimates for *Chalinolobus tuberculatus* from New Zealand (O'DONNELL, 2002), but in the range of estimates for microchiropterans from the Northern Hemisphere such as *Eptesicus fuscus* (MILLS et al., 1975), and *Myotis myotis* (ZAHN, 1999).

ALDRIDGE et al., (1990) and CHURCHILL et al., (1997) provided limited data on the roosting habits of *Nycteris thebaica*, while FENTON et al., (1987), based on a sample of five adults, showed that *Nycteris grandis* may exhibit roost fidelity. In contrast, this paper is the first to report on roost occupancy and fidelity for any Nycteridae based on a large number of banded individuals surveyed over several breeding seasons. Female *Nycteris thebaica* exhibited roost site fidelity returning to the same culvert or neighbouring set of culverts. This is despite the relative proximity of the fifteen culverts. *Nycteris thebaica*, therefore, appears to be a sedentary species with females forming groups of fairly stable composition.

The formation of groups of stable composition has also been observed in other African bats including *Myotis bocagii* (BROSSET, 1976), *Coleura afra* (MCWILLIAM, 1987), *Tadarida pumila* (MCWILLIAM, 1988) and in non-African species such as *Chalinolobus tuberculatus* (O'DONNELL, 2002). Roost fidelity has been observed in several African microchiropterans including *Hipposideros commersoni* (VAUGHAN, 1977), *Rhinolophus hildebrandti* and *Tadarida midas* (FENTON & RAUTENBACH, 1986), *Coleura afra* (MCWILLIAM, 1987), *Tadarida pumila* (MCWILLIAM, 1988) and male *Pipistrellus nanus* (HAPPOLD & HAPPOLD, 1996). In contrast, *Scotophilus leucogaster* (FENTON, 1983) and *S. viridis/S. borbonicus* (FENTON et al., 1985) regularly switch day roosts.

Male *Nycteris thebaica* exhibited less roost site fidelity than females. Movement between roosts was greater in males than females. Males, therefore, appeared not to be tied down to one particular culvert or group of adjacent culverts. This was illustrated by the fact that a male *Nycteris thebaica* originally banded at a different location was recaptured at this study site, representing a distance of approximately 9 km.

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REFERENCES

ALDRIDGE, H.D.J.N., M. OBRIST, H.G. MERRIAM & B. FENTON (1990). Roosting, vocalizations, and foraging by the African bat, *Nycteris thebaica*. *J. Mammal.*, 71 : 242-246.

BOWIE, R.C.K., D.S. JACOBS & P.J. TAYLOR (1999). Resource use by two morphologically similar insectivorous bats (*Nycteris thebaica* and *Hipposideros caffer*). *S. Afr. J. Zool*., 34 : 27-33.

BROSSET, A. (1976). Social organization in the African bat, *Myotis bocagei. Zeitschrift fur Tierpsychologie*, 42 : 50-56.

CHURCHILL, S., R. DRAPER & E. MARAIS (1997). Cave utilization by Namibian bats : population, microclimate and roost selection. *S. Afr. J. Wildl. Res*., 27 : 44-50.

CLARKE, K.R. & R.N. GORLEY (2001). *Primer v5 : user manual.* Plymouth Marine Laboratory, Plymouth.

FENTON, M.B. (1983). Roosts used by the African bat, *Scotophilus leucogaster* (Chiroptera : Vespertilionidae). *Biotropica*, 15 : 129-132.

FENTON, M.B., R.M. BRIGHAM, A.M. MILLS & I.L. RAUTENBACH (1985). The roosting and foraging areas of *Epomophorus wahlbergi* (Pteropodidae) and *Scotophilus viridis* (Vespertilionidae) in Kruger National Park, South Africa. *J. Mammal*., 66 : 461-468.

FENTON, M.B., D.H.M. CUMMING, J.M. HUTTON & C.M. SWANEPOEL (1987). Foraging and habitat use by *Nycteris grandis* (Chiroptera : Nycteridae) in Zimbabwe. *J. Zool., Lond.*, 211 : 709-716.

FENTON, M.B. & I.L. RAUTENBACH (1986). A comparison of the roosting and foraging behaviours of three species of African insectivorous bats (Rhinolophidae, Vespertilionidae, and Molossidae). *Can. J. Zool.*, 64 : 2860-2867.

HAPPOLD, D.C.D. & M. HAPPOLD (1990). The domiciles, reproduction, social organization and sex ratios of the Banana Bat, *Pipistrellus nanus* (Chiroptera : Vespertilionidae) in Malawi, Central Africa. *Zeitschrift fur Saugetierkunde*, 55 : 145-160.

HAPPOLD, D.C.D. & M. HAPPOLD (1996). The social organisation and population dynamics of leaf-roosting banana bats, *Pipistrellus nanus* (Chiroptera : Vespertilionidae), in Malawi, east-central Africa. *Mammalia*, 60 : 517-544.

LAVAL, R.K. & M.L. LAVAL (1977). Reproduction and behaviour of the African Banana Bat, *Pipistrellus nanus*. *J. Mammal.*, 58 : 403-410.

MCWILLIAM, A.N. (1987). The reproductive and social biology of *Coleura afra* in a seasonal environment. In : FENTON, M.B., P. RACEY & J.M.V. RAYNER (eds), *Recent advances in the study of bats*. Cambridge University Press : 324-350.

MCWILLIAM, A.N. (1988). Social organization of the bat *Tadarida (Chaerephon) pumila* (Chiroptera : Molossidae) in Ghana, West Africa. *Ethology*, 77 : 115-124.

MILLS, R.W., G.W. BARRETT & M.P. FARRELL (1975). Population dynamics of the big brown bat (*Eptesicus fuscus*) in southwestern Ohio. *J. Mammal*., 56 : 591-604.

MONADJEM, A. (1998). *Mammals of Swaziland*. The Conservation Trust of Swaziland and Big Game Parks, Mbabane.

MONADJEM, A. (2001). Sexual dimorphism, sex ratio and preliminary recapture rates of *Nycteris thebaica* (Nycteridae : Chiroptera) in Swaziland. *Durban Mus. Novit*, 26 : 49-52.

O'DONNELL, C.F.J. (2000). Cryptic local populations in a temperate rainforest bat *Chalinolobus tuberculatus* in New Zealand. *Anim. Conserv.*, 3 : 287-297.

O'DONNELL, C.F.J. (2002). Timing of breeding, productivity and survival of long-tailed bats *Chalinolobus tuberculatus* (Chiroptera : Vespertilionidae) in cold-temperate rainforest in New Zealand. *J. Zool., Lond.*, 257 : 311-323.

O'SHEA, T.J. (1980). Roosting, social organization and annual cycle in a Kenya population of the bat *Pipistrellus nanus*. *Zeitschrift fur Tierpsychologie*, 53 : 171-195.

SEAMARK, E.C.J. & W. BOGDANOWICZ (2002). Feeding ecology of the common slit-faced bat (*Nycteris thebaica*) in KwaZulu-Natal, South Africa. *Acta Chiropterologica*, 4 : 49-54.

SMITHERS (1983). *The mammals of the southern African subregion*. University of Pretoria, Pretoria.

SWIFT, S.M. (1998). *Long-eared bats*. T & AD POYSER, Natural History, London.

TAYLOR, P.J. (1998). *The smaller mammals of KwaZulu-Natal*. University of Natal Press, Pietermaritzburg.

TAYLOR, P.J. (2000). *Bats of southern Africa*. University of Natal Press, Pietermaritzburg.

VAN DER MERWE, M. (1989). Longevity in Schreibers' long-fingered bat. *S. Afr. J. Wildl. Res.*, 19 : 87-89.

VAUGHAN, T.A. (1977). Foraging behaviour of the giant leaf-nosed bat (*Hipposideros commersoni)*. *East African Wildlife Journal*, 15 : 237-249.

WICKER, W. & D. UHRIG (1969). Verhalten und okologische nische der gelbflugelfledermaus *Lavia frons* (Geoffroy) (Chiroptera, Megadermatidae) *Zeitschrift fur Tierpsychologie*, 26 : 726-736.

ZAHN, A. (1999). Reproductive success, colony size and roost temperature in attic-dwelling bat *Myotis myotis*. *J. Zool., (Lond.)*, 247 : 275-280.

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Effects of habitat fragmentation on diversity of small mammals in Lulanda Forest in Mufindi, Tanzania

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ABSTRACT. The Lulanda forest cover a portion of the Udzungwa mountains in Mufindi district, Tanzania, ranging from 1480 – 1640 meters above sea level. The forest consists of three forest patches dominated by *Parinari excelsa* and a corridor between two of them that is being regenerated to a forest under the help of the Tanzania Forest Conservation Group (TFCG). A capture-mark-recapture study was carried out to document the small mammal species found in Lulanda forest patches and corridor. There is a considerable difference in small mammal species composition between the montane forest and the corridor with a higher diversity in the corridor.

KEY WORDS : Small mammals, Habitat fragmentation, Forest patches and Corridor

INTRODUCTION

The Udzungwa Mountains are part of the Eastern Arc Mountains (EAM), a chain of isolated mountain groups that run from Taita hills in Kenya to Udzungwa Mountains in southern Tanzania (LOVETT & CONGDON, 1990). The mountains have been recognized as one of the 25-biodiversity hotspots in the world (MYERS et al., 2000). Rapid increase of the human population, acquired needs from forests such as farmland, timber, firewood, and medicinal plants cause an overall loss of forest habitat and fragmentation of the remaining area (RODGERS, 1998). Anthropogenic alteration of habitat is therefore affecting whole ecosystems and biota, particularly forest around the equator where hotspots are centred (MYERS et al., 2000). When habitats such as forest undergo fragmentation, remnant patches of the habitat are increasingly isolated in a matrix of altered and often heavily used lands (GROOMBRIDGE, 1992). Habitat loss and fragmentation are major threats to the viability of populations and have been shown to be good predictors of extinction threats in biodiversity hotspots (BROOKS et al., 1999, FERRERAS, 2001). Fragmentation of these habitats isolates also small mammal populations (BROOKS et al., 1999). For example, the high degree of anthropogenic forest fragmentation in the Taita Hills, also part of the Eastern Arc Mountains, most likely added to differential extinction (CORDEIRO, 1998).

In this study we define small mammals as non-flying mammals weighing less than 1kg when adult (BARNETT & DULTON, 1995). Small mammals provide food for avian and mammalian predators while, at the same time being important consumers of seeds and herbage. Therefore, small mammals are important contributors to biodiversity of woodland-savannah ecosystem in sub-Saharan Africa and good ecological indicators (LINZEY & KESNER, 1997).

Although many researchers have worked on the overall biodiversity richness of the EAM, little is known on the small mammal diversity of specific forest patches and corridors between them in the Udzungwa Mountains. This paper presents part of a wider study aimed at documenting the animal species found in the Lulanda forest patches and corridor. Our interest was to observe the effect of habitat fragmentation to the diversity of small mammals and the role of corridor rehabilitation on supporting the diversity of forest patches.

METHODS

Study area

The Lulanda forest is located in the southern Udzungwa mountains (5km east of Mufindi Escarpment East Forest Reserve) in two valleys on the edge of the east-facing escarpment from 1480 – 1640 meters above sea level. The forest consists of three forest patches and a corridor between two of them. Fufu forest patch has an area of 89.3 ha (approximately 1000m x 600m), Magwila an area of 82.6 ha (approximately 1100m x 400m), and the corridor linking Fufu and Magwila is 54 hectares. The Tanzania Forest Conservation Group is regenerating the corridor by replanting the indigenous trees in the area that was formerly covered by farmland, and the replanted trees were six years old at the time of the study.

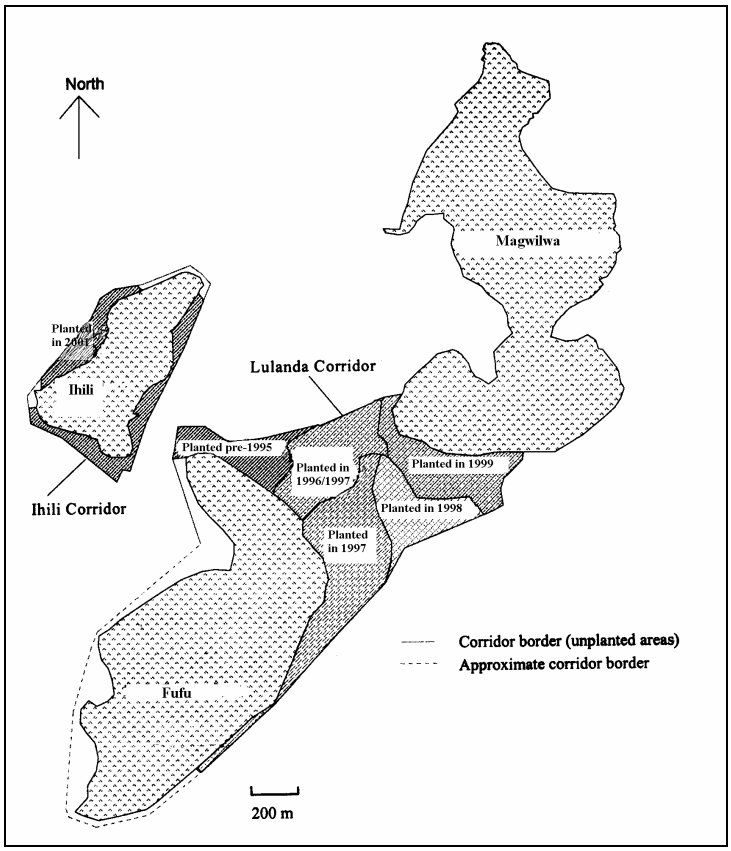

Fig. 1. – A map showing the location of Lulanda forest (after DOODY, 2002)

The forest patches are dominated by *Parinari excelsa* with swampy open areas in valley bottoms. Canopy is up to 30m, intact in parts but generally much disturbed following extraction of timber species in the past (LOVETT & CONGDON, 1990). All areas have undergone disturbances but there is no evidence that the forest patches have ever been completely cleared, so the majority is primary forest. The surrounding habitat is farmland with the major crop being maize. There is encroachment along the edges of the forest for cultivation, and the collection of building poles, firewood and medicinal plants. A footpath through the forest links the village with cultivated areas.

In order to study the effect of habitat fragmentation on the diversity of small mammals, trapping programs were carried out for these animals in two trapping sites in each study area (i.e. Fufu, Magwila and the corridor).

Trapping design

Each trap site (Fufu, Magwila and corridor) consisted of four bucket pit-fall lines running parallel 50m apart following a methodology used by STANLEY et al., (1996). Each line consisted of 10 buckets buried in soil so that the rim was flush with the ground trapping points were 5m apart. A drift fence of clear plastic sheet of approximately 50cm was erected bisecting each bucket along the length of the line. Twenty medium Sherman traps (23 cm x 9.5 cm x 8 cm) were placed at each side of the fence at 5m intervals. The lines were laid out in such away that they minimized a possible edge effect of boundaries between forest, corridor and adjacent cultivated land.

Two prebaiting nights were conducted before the commencement of trapping in order to reduce trap shyness. There was a total of 120 bucket-pit fall trap-nights and 240 Sherman trap-nights. A mixture of peanut butter and maize flour was used as bait. All traps were checked both at dawn and dusk. However traps in the corridor were left closed during the day as it was felt that they were exposed to high temperatures.

For surveying small primates (bushbabies), suitable habitats containing vines and climbers were identified. Three wire mesh traps (30 cm x 30 cm x 45 cm) were placed approximately 1.5m above ground level more than 500m apart. Bananas and bamboo wine were used as bait; bananas were also smeared on surrounding branches and vines. Sixty trap-nights were conducted in two areas (Fufu and Magwila forest patches). The captured mammals were fur clipped for capture-mark-recapture (BARNETT & DUTTON, 1995).

For the purpose of this study we used species richness given by the total number of species occurring in an area and local diversity as expressed by the Shannon-Wiener and Simpson indices (KREBS, 1989).

The Shannon Index (H) is given by,

$$H = -\sum_{i=1}^{s} (P_i)(\ln P_i)$$

Where S= Number of species,

P_i=Proportion of individuals of the total sample belonging to the i^{th} species.

The Simpson index of diversity (D) is equal to the probability that two randomly picked organisms belong to the same species. It is given by :

$$D = 1-\sum_{i=1}^{s} (P_i)^2$$

where P_i = Proportion of individuals belonging to the i^{th} species in the community.

The index of similarity between areas was calculated as 2z/(x+y), where x and y are the number of species occurring in each patch and z the number of species occurring in both patches.

RESULTS

A total of 45 small mammals were caught in bucket pit falls, 124 in Sherman traps and 8 in bushbaby traps (tables1-3). Mammals caught were from 10 genera (seven rodents, two insectivores and one primate). Exact species identification was not possible since the animals were released after trapping. The most commonly trapped mammal in both forest patches was *Praomys sp*, with about 49.5% of all individuals recorded. However, only one individual of this species was trapped in the corridor. *Mus sp.* was the most encountered genus in the corridor accounting for 42.1% of individuals trapped in the corridor. *Grammomys sp.* and *Crocidura sp.* were also represented in higher numbers (36.8%) within the corridor; *Grammomys sp.* was not recorded at all in either forest patch. Certain genera were caught only in the forest patches, including *Hylomyscus* and *Beamys sp.*. Two *Beamys* were caught in bushbaby traps (one in Fufu, one in Magwila) and one in Sherman trap in Magwila. As noted in the methodology, Sherman traps in the corridor were closed during the day; therefore diurnal species were only caught in the forest patches. Six Grant's galago (*Galagoides grantii*) were trapped in the Fufu forest patch in the wire mesh traps and none in the Magwila forest patch (however they were excluded in diversity indices calculations since they are at the upper weight level of what should be considered small mammals.

In terms of local species richness, Magwila was the highest in richness with seven species followed by both Fufu and the corridor with six species each. The Shannon Index of the three sites were : 2.145, 1.421 and 1.275 for the corridor, Fufu and Magwila respectively. The highest dominance/Simpson index was found in the corridor (D=0.731) followed by Fufu forest patch (D=0.42). The lowest dominance index was recorded in the Magwila forest patch (D=0.369). The obtained similarity indices were between corridor and Fufu 0.667, between the corridor and Magwila 0.769 and between Fufu and Magwila 0.769.

TABLE 1

Captures of small mammals in pitfall, by genus and site.

Genera	Corridor	Fufu	Magwila
Dendromus	7	0	3
Crocidura	9	6	4
Mus	3	5	4
Praomys	0	2	2
Lophuromys	0	0	0

TABLE 2

Captures of small mammals in Sherman traps, by genus and site.

Genus	Corridor	Fufu forest	Magwila
Dendromus	0	0	0
Crocidura	12	0	0
Mus	21	1	0
Praomys	1	69	37
Lophuromys	4	10	8
Grammomys	10	0	0
Hylomyscus	0	5	0
Beamys	0	0	1

TABLE 3

Captures of small mammals in bushbaby traps, by genus and site.

Genus	Fufu	Magwila
Galagoides	6	0
Beamys	1	1

DISCUSSION

The TFCG corridor regeneration program is expected to have a positive effect on the Lulanda forest reserve. At this stage of succession six years after replanting work started, the corridor already supports a diverse small mammal community. Although five mammal genera were represented in both the forest and the corridor, the genera composition of the corridor differed from that of the forest patches. *Praomys* appeared to be the dominant small mammal genus in both forest patches, in contrast to the corridor where *Praomys* was only caught once and there were no other apparent dominant genera. Several species were met in only one of the forest patches (e.g. *Hylomyscus* sp., *Galagoides grantii*) and it is possible that fragmentation still blocked the migration route for this species from Fufu to Magwila, e.g. because of the arboreal life of the bushbabies.

The Shannon indices suggested that the corridor is more diverse followed by Fufu then Magwila forest patches. The inverse results between species richness and diversity is attributed to the fact that species diversity considers both richness and evenness of species in a particular area. The Simpson index of diversity (D) measures the distribution of the individuals among the species in a community (MALIMBWI et al., 1998). Magwila, which had the highest number of species, is the least when consider-

ing species dominance; this is attributed to the imbalances in species distribution/species evenness.

The three sites show fairly high similarity indices among them, perhaps because of the relatively small area over which the study was carried out.

Our findings suggest that the corridor is in the early stages of succession when compared to the rather climax communities of the forest patches. Similar studies needs to be carried out periodically in the study area and in other parts of the eastern arc mountains, paying attention also to agricultural and settled areas surrounding the remaining forests, so as to come out with the effect of habitat fragmentation on the diversity of small mammals in the entire archipelago.

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REFERENCES

BARNETT, A. & J. DUTTON (1995). Expedition Field Techniques : Small Mammals. *Royal Geographic Society (with the Institute of British Geographers),* London, 126 pp.

BROOKS, T.M., S.L. PIMM & J.O. OYUGI (1999). Time lag between deforestation and bird extinction in tropical forest fragments. *Conservation Biology*, 13 : 1140–1150.

CORDEIRO, N.J. (1998). A preliminary survey of the Montana avifauna of Mt. Nilo, East Usambaras, Tanzania. *Scopus*, 20 : 1-18.

DOODY, K. (2002). An assessment of a reforestation programme in the Southern Udzungwa Mountains, Tanzania. *Tanzania Forest Conservation Group Technical Report 3.*

FERRERAS, P. (2001). Landscape structure and asymmetrical inter-patch connectivity in a metapopulation of endangered Iberian lynx. *Biological Conservation*, 100 : 125-136.

GROOMBRIDGE, B. (ed) (1992). *Global biodiversity assessment. Status of the Earth's Living Resources*. Chapman and Hall, London, 585 pp.

KREBS, C.J. (1989). *Ecological methodology.* Harper Collins Publishers, New York, 554 pp.

LINZEY, A.V. & M.H. KESNER (1997). Small Mammals of Woodland Savannah Ecosystem in Zimbabwe, Density and Habitat occupancy Patterns. *Journal of Zoology*, London 243 : 137-152.

LOVETT, J.C. & T.C.E. CONGDON (1990). Notes on Lulanda Forest, sourthern Udzungwa mountains. *East Africa Natural History Society Bulletin*, 20 : 21.

MALIMBWI, R.E., J. KIELAND-LUND, J. NDUWAMUNGU (1998). Species diversity and standing crop development in four miombo vegetation communities. In : CHAMSHAMA, S.A.O. (ed), Proceedings of the First Annual Forest Workshop. Faculty of Forestry, SUA, Morogoro. pp. 201-212.

MYERS, N., R.A. MITTERMEIER, C.G. MITTERMEIER, G.A.B. DA FONSECA & J. KENT (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403 : 853-858.

RODGERS, W.A. (1998). An introduction to the conservation of the Eastern Arc Mountains. *J.East Afr. Nat. Hist.*, 87 : 7-18.

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 Macroscelidea*). Zool. Abh. (Dresden)*, 49 : 131-147.

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Community structure and seasonal abundance of rodents of maize farms in Southwestern Tanzania

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ABSTRACT. Community characteristics and seasonal abundance of rodents were investigated in a small-scale maize field-fallow land mosaic in southwestern Tanzania between February 2001 and May 2002. During the study, a total of 2568 rodents were captured in 9150 trapnights giving a 28% trap success. Also shrews of the genus *Crocidura* (Soricidae) were recorded. *Mastomys natalensis* comprised the highest proportion of rodents caught accounting for 82.9% of all captures. Other rodent genera captured included : *Tatera, Saccostomus, Graphiurus,* and *Steatomys*. Relative densities as measured by both trap success and the number of rodents per hectare, and biomass varied between seasons with and without crop in the field but not between habitat types. The work reports seasonality in breeding for the two most commonly trapped species, *Mastomys natalensis* and *Tatera leucogaster.*

KEY WORDS : rodents, community structure, seasonal abundance, refuge habitat, Africa

INTRODUCTION

Outbreaks of rodents over large areas have been reported in many areas in Africa; however, considerable damage to agriculture has also been reported in non-outbreak years (FIEDLER, 1988, 1994). In eastern Africa, especially in small-scale farms and marginal landscapes, field rodents are a very serious concern after drought and poor soils as a major constraint to improved yield of staple crops. Rodent damage particularly to cereal crops remains a chronic problem among small-scale farmers in this region. However, quantitative information on the type and level of damage remains descriptive. Earlier reports of maize losses due to rodents shows damages of up to 20% annually in Kenya (TAYLOR, 1968; also reviewed in OGUGE et al., 1997) and Ethiopia (GOODYEAR, 1976). TAYLOR (1968) reported that during rodent outbreaks in Kenya, maize losses could be as high as 34 to 100%.

For Tanzania, the average annual yield loss of maize is estimated to be around 5 to 15% (MAKUNDI et al., 1991). This corresponds to more than 400,000 tonnes of maize, equivalent to an amount that could feed 2.3 million people for a whole year (LEIRS, 2003). Besides the usual annual losses in Tanzania, irregular rodent outbreaks occur during which damage to crops can increase to over 80% (LEIRS et al., 1996; MWANJABE & LEIRS, 1997).

In Tanzania, agricultural fields are situated in a matrix of surrounding habitats which in smallholder settings is most often fallow land. These habitats change seasonally leading to a spatial component of the community and population dynamics of organisms living in these fields (LEIRS et al., 1997b). The fallow lands are said to provide a suitable ground for shelter and breeding for rodents while grass and weed seeds provide supplementary food (MWANJABE, 1993). Fallow land matrix has also been assumed to act as refuge for rodents in the maize field during unfavourable conditions. As such it is expected that rodents that inhabit the maize fields will dissipate into the fallow land and return only during the attractive crop stages. This means that during the unfavourable periods, rodent densities will be higher in the surrounding matrix than in the maize field and vice versa during the attractive periods. A sound understanding of community dynamics in the farm lands and the surrounding matrix may allow to predict changes in rodent densities and community structure, which is of prime importance for the development of species and/or community specific management strategies.

In the present paper, we investigate community structure and seasonal abundance of rodents of maize farms and their surrounding matrix in southwestern Tanzania. We hypothesize that, rodents in the maize field move to the surrounding matrix during the unfavourable crop stages and vice versa during the attractive stages leading to a marked difference in densities in the two habitats at the different crop stages.

MATERIAL AND METHODS

The study took place in Chang'ombe village of Chunya district, which is located in southwestern Tanzania between 07° 58'S – 33° 18'E and 08° 46'S - 33° 18'E. The climate of the area is dry subhumid with annual rainfall of about 900mm. Rainfall is unimodal with peak precipitation between November and March. Although rainfall is variable between years, it is relatively reliable.

We selected two sites for the placement of our removal grids. These sites were denoted as Chunya1 and Chunya2. At each of the two removal grids, 75 snap traps and 75 Sherman traps were used, giving a total of 150 trap stations. Of the 150 trap stations per grid, 50 trap stations were placed within the target crop (maize) while the other 100 trap stations were placed in the matrix habitat. The traps were placed in lines on which traps were spaced 10m apart. Within the target crop each of the 5 trap lines (10 traps/line) were spaced 10m apart while the 5 trap lines outside the target crop (20 traps/line) were spaced 40m apart up to 200 m from the edge of the crop. During trapping sessions, snap traps and Sherman traps were placed alternating in each trap line. The trap positions were marked with painted bricks so that the locations could be used during subsequent trapping. The traps were baited with a mixture of peanut butter and maize scrap. The two grids were about 3km apart. Animals were trapped during the different crop stages : a) at least one month before planting b) planting/after planting c) seedling stage d) vegetative/middle of growth stage e) before harvesting/ripe stage and f) at least one month after harvest. During these sessions, trapping was carried out for three consecutive days.

Trapped animals were identified, weighed, sexed and measured. The body condition (visible injury, ectoparasites) and reproductive condition were also noted. In addition, the point of capture, date and weather conditions were recorded. Processed specimens were preserved in 10% buffered formalin. Live-trapped animals were sacrificed under diethyl ether before processing.

For purposes of description and analysis, rodent community is defined as all trappable rodent species occurring in the study sites. Description of seasonal abundance and community composition is based on trapped individuals. Rodent abundance is expressed as 1) percent trapping success i.e. the proportion of captures relative to the number of traps set over a given period (TELFORD, 1989) and, 2) density estimates; rodent captures per given area. A chi-square (χ^2) test was used to inspect any differences in sex ratios. Biomass is based on the total weights of the different rodents captured and is expressed in relation to the studied area.

RESULTS

Rodent species composition

A total of 2568 captures of five species of rodents were made in 9150 trap nights. Also shrews of the genus *Crocidura* were caught during this study. The five species of rodents recorded were *Mastomys natalensis* (82.9%), *Tatera leucogaster* (15.9%), *Saccostomus campestris* (0.8%), *Graphiurus murinus* (0.2%) and *Steatomys* sp. (0.2%) (Table 1).

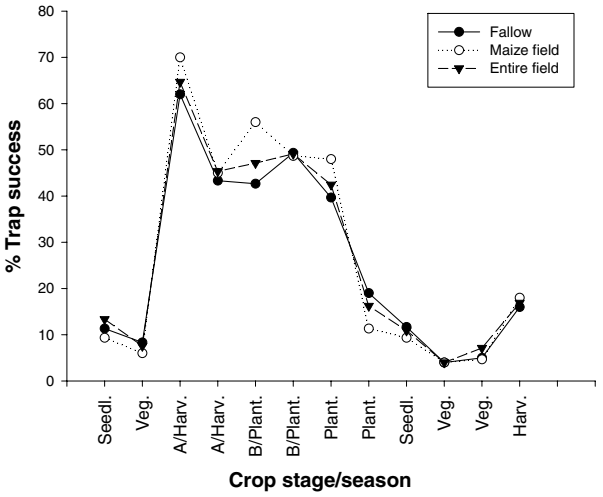


Fig. 1. – Trap success for the different crop stages/seasons in southwestern Tanzania.

TABLE 1

Rodent species composition in Chunya, southwestern Tanzania

Species	Chunya1	Chunya2	Totals	% contribution
Mastomys natalensis	946	1176	2122	82.9
Tatera leucogaster	300	103	403	15.9
Steatomys sp.	6	0	6	0.2
Graphiurus murinus	4	2	6	0.2
Saccostomus campestris	1	20	21	0.8
Totals	1257	1301	2558	100

Trap success

The mean trap success for Chunya1 and Chunya2 combined was 28%. Trap success varied greatly throughout the study being lowest in February/March during the vegetative stage and highest in July/August, three months after harvesting and before planting (Fig. 1). In most trapping sessions, trap success was higher for rats in the fallow land than for those in the maize field. However, the differences were small, inconsistent and insignificant ($t = -0.166$, $df = 22$, $P = 0.869$). Trap success differed significantly between seasons with and without crops on the field ($F_{5, 120} = 20.99$, $p < 0.001$), but not between both habitat types and there was no interaction between season and habitat type.

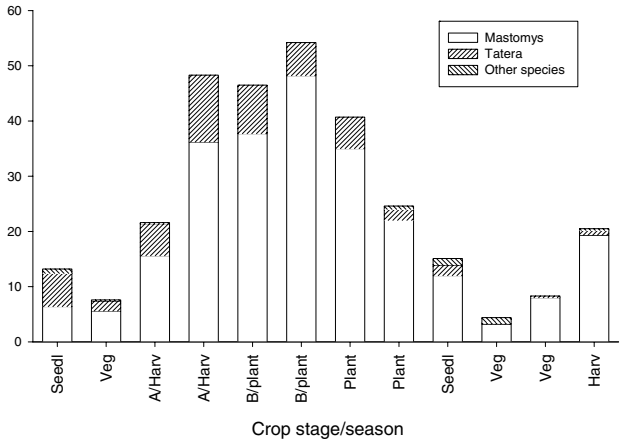


Fig. 2. – Seasonal relative densities of the different rodent taxa in maize fields in southwestern Tanzania.

Density patterns

The total rodent densities varied in the different crop seasons. Densities ranged between 4 animals per hectare during the vegetative period of February/March and 54 animals per hectare just before land preparation and planting in September/October (Fig. 2). This same trend was recorded for animals caught both in the maize field and fallow land. However, relative densities were always higher in maize compared with fallow. Densities in maize ranged between 12 and 156 animals per hectare while those in the fallow area were 3 to 41 animals per hectare. In Chunya1, the overall densities ranged from 4 to 49 animals per hectare. Fallow recorded lower densities (3-37/ha) than in the maize (6-84/ha) (Figs 3a&b). In Chunya2, the overall relative density was 5-59 animals per hectare. Again here fallow recorded lower densities (4-45/ha) than maize (12-162/ha) (Figs 3c&d). Relative densities differed significantly between seasons with and without crop on the field ($F_{5, 120} = 18.03$, $p < 0.001$) but not between both habitat types.

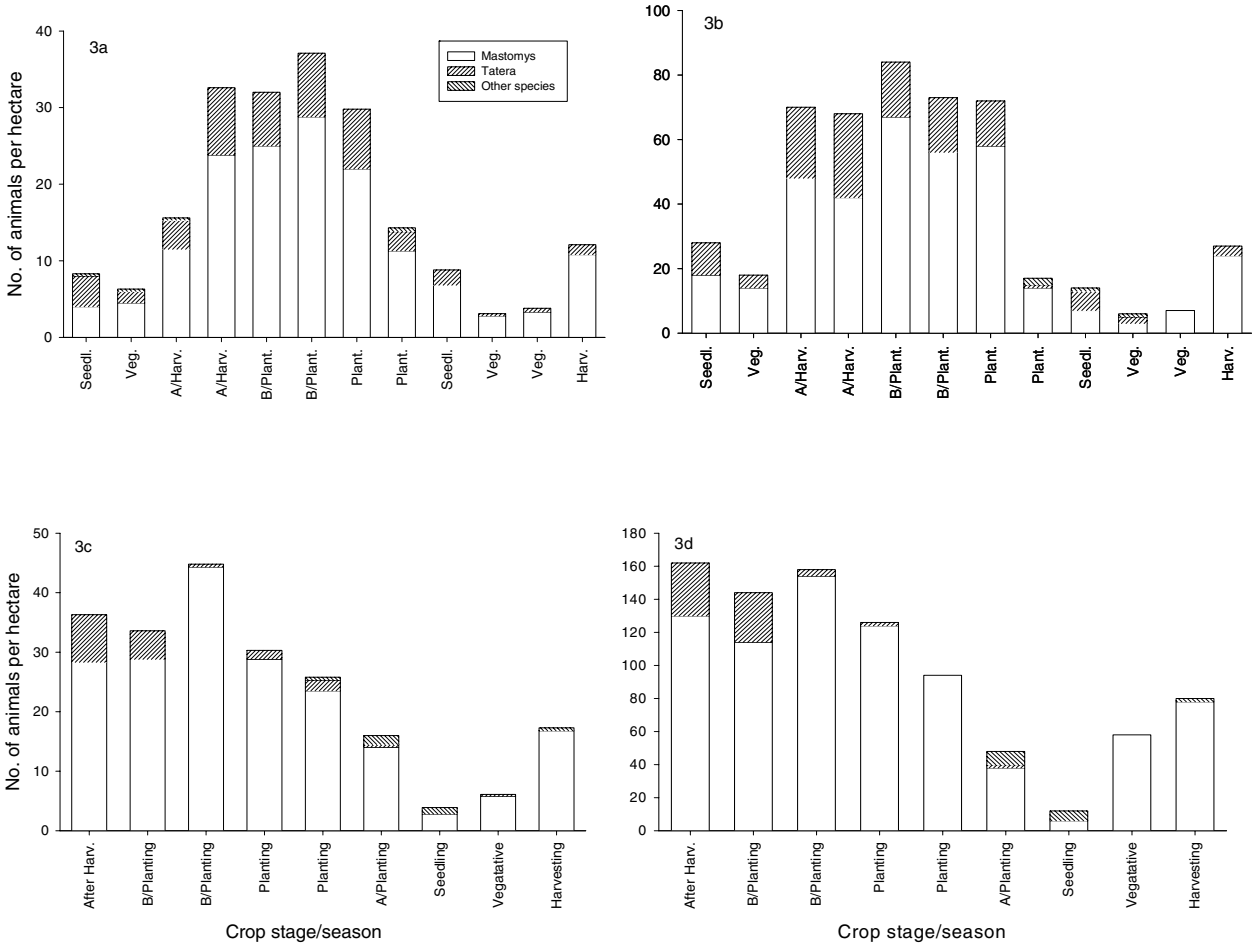


Fig. 3. – Seasonal relative densities of rodents
a) in Chunya 1 fallow land; b) in Chunya 1 maize farm; c) in Chunya 2 fallow land; d) in Chunya 2 maize farm

Biomass

The seasonal weight of the total number of rodents captured in the 4.5 ha grids varied from 923 to 9246g (205-2055g/ha). Except for February 2001 (vegetative stage) when *Tatera* recorded equal biomass with that of *Mastomys*, *Mastomys natalensis* formed the largest biomass on all trapping occasions accounting for as high as 86.2% of the total biomass in April (Table 2). In most seasons, biomass was higher for rodents in the fallow land than those in the maize crop. However, again here as with trap suc-

cess the differences were small, inconsistent and insignificant ($t = -1.13$, $df = 32$, $P = 0.26$). Biomass differed significantly between seasons with and without crops on the field ($F_{4, 120} = 24.98$, $p < 0.001$), but not between both habitat types and there was no interaction between season and habitat type.

TABLE 2

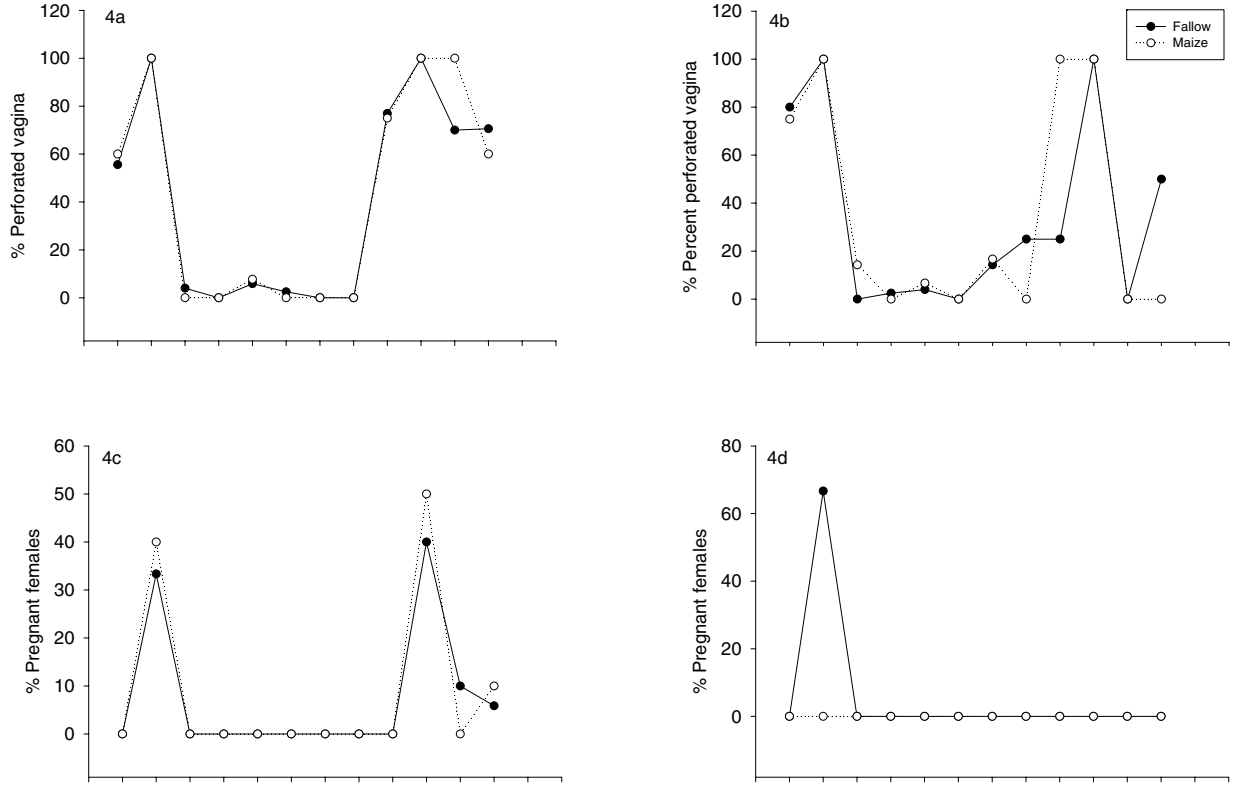
Total biomass (g/4.5ha) of rodents and other small mammals in Chunya (% contribution are given in parentheses).

Month	Mastomys	Tatera	Steatomys	Graphiurus	Saccostomus	Crocidura	All species
February 2001	1612 (43.5)	1970 (53.1)	63 (1.7)	38 (1.0)	0	24 (0.6)	3709
March 2001	1257 (62.9)	710 (35.5)	0	28 (1.4)	0	0	1999
July 2001	2945 (60.6)	1854 (38.1)	0	24 (0.5)	0	41 (0.8)	4862
August 2001	4915 (53.1)	4331 (46.8)	0	0	0	0	9246
September 2001	4887 (62.2)	2964 (37.7)	0	0	0	0	7851
October 2001	5637 (65.0)	3038 (35.0)	0	0	0	0	8675
November 2001	3975 (58.7)	2796 (41.3)	0	0	0	0	6771
December 2001	1959 (69.0)	799 (28.1)	62 (2.2)	0	0	19 (0.7)	2839
January 2002	1606 (58.5)	1141 (41.5)	0	0	32 (1.2)	0	2747
February 2002	951 (78.5)	238 (19.6)	0	0	0	0	1211
April 2002	796 (86.2)	127 (13.7)	0	0	0	0	923
May 2002	2804 (82.8)	539 (15.9)	0	0	0	42 (1.2)	3385

Reproduction

Of the rodents trapped, 1177 (46.0%) were males, 1063 (41.6%) were females while 318 (12.4%) were unsexed. The sex ratios (male :female) of *Tatera leucogaster* (170 :191), *Saccostomus campestris* (12 :9), *Graphiurus murinus* (2 :4) and *Steatomys* sp. (2 :4) were all of the expected one-to-one (1 :1) ratio. In overall more males of *Mastomys natalensis* (991 :855) were caught than females ($\chi^2 = 5.0097$, $p < 0.05$) (Table 3). However, the seasonal sex ratio of *M. natalensis* was not significantly different from the expected 1 :1 ratio.

Reproductive activity was highly seasonal in *M. natalensis* and *T. leucogaster*, which were the only species caught in appreciable numbers. This seasonality in breeding was similar in both habitat types. Females of *M. natalensis* had a high proportion of females with perforated vagina around March during the vegetative stage of crop; this is followed by a long period of non-reproductive activity (Fig. 4a). The same reproductive pattern was witnessed in *T. leucogaster* (Fig. 4b). Females of *M. natalensis* and *T. leucogaster* are pregnant (Figs 4c&d) or lactating (Figs 4e&f) around February, March and April thereafter reproduction is suspended.



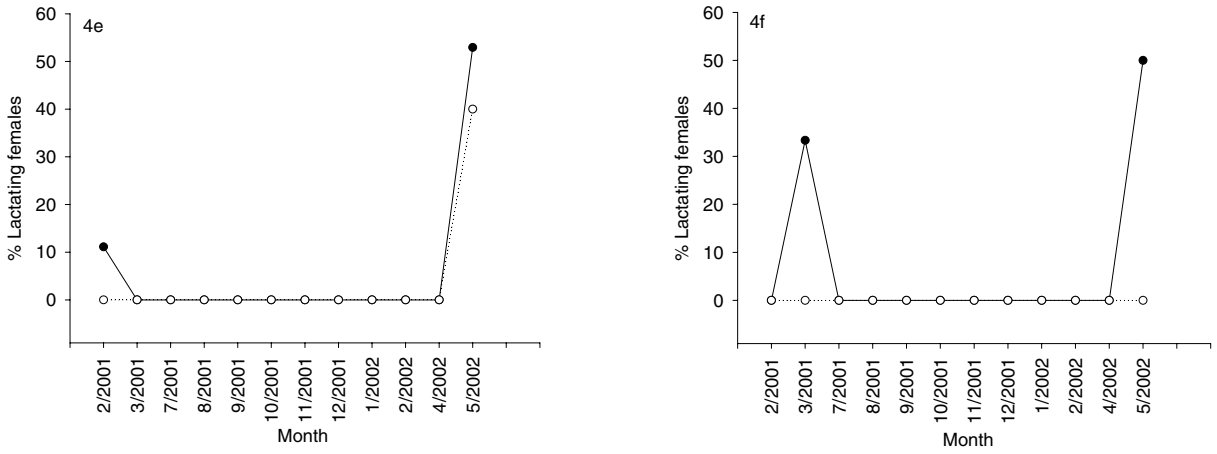


Fig. 4. – Reproductive characteristic of *M. natalensis* and *T. leucogaster* in fallow land and maize field
a) Proportion of female *M. natalensis* with perforated vagina; b) Proportion of *T. leucogaster* with perforated vagina; c) Proportion of visibly pregnant *M. natalensis;* d) Proportion of visibly pregnant *T. leucogaster;* e) Proportion of lactating *M. natalensis;* f) Proportion of lactating *T. leucogaster.*

TABLE 3

Sex ratio of rodent species caught in southwestern Tanzania (NS = not significant)

Species	Males	Females	χ^2	Significance
Mastomys natalensis	991	855	5.0097	$P < 0.05$
Tatera leucogaster	170	191	0.6108	NS
Steatomys sp.	2	4	0.3333	NS
Graphiurus murinus	2	4	0.3333	NS
Saccostomus campestris	12	9	0.2143	NS

DISCUSSION

On a seasonal (crop stage) scale, we found no differences in trap success, relative densities and biomass of rodents in fallow land and maize field. There were animals in the maize fields during the different crop seasons and their relative abundance varied seasonally just like that in the surrounding matrix. Likewise, we did not find any evidence of the fallow land acting as a refuge for rodents during the non-attractive crop stages nor did the data report of animals leaving the fallow land to the maize field during the attractive stages. The same density patterns were recorded for both fallow land and maize field. There is a large turnover in the densities of rodents across time in both the maize field and fallow land. This type of scenario has also been reported in a study of *Mastomys natalensis* in a maize field-fallow mosaic in Morogoro, Tanzania (LEIRS et al., 1997b)

The lowest densities were recorded in February/March during the vegetative period of the crop. Densities start rising steadily in May and peak densities are recorded in September/October, two to three months before planting. This density pattern appeared not to be related with the crop stage rather it could be explained by the fact that the first pregnant females were observed by the end of February (vegetative stage) so that an increase in numbers is not expected before the second half of April. Indeed numbers start increasing by May. Our density estimates are rather low compared to reported densities for Tanzania and elsewhere (LEIRS, 1995 and references therein) where up to a thousand animals per hectare have been reported in outbreak periods, with normal peaks of several hundreds in studies involving *Mastomys* spp. TELFORD (1989) reported a density estimate of 1125 animals/ha while LEIRS (1995) reported densities of 900 animals/ha and CHRISTENSEN (1996) reported densities of 384 animals/ha in Morogoro, Tanzania. Our densities of 3 – 162 animals/ha compare well with those obtained in studies in Kenya (ODHIAMBO & OGUGE, 2003) and Ethiopia (BEKELE & LEIRS, 1997; BEKELE, et al., 2003). These findings are however not surprising given the fact that *M. natalensis* comprised the highest percentage of rodents captured. The population dynamics of this species is known to be influenced by both density dependent and density-independent factors occurring simultaneously (LEIRS et al., 1997a). Moreover, its breeding characteristics are strongly dependent on the amount of rainfall (LEIRS et al., 1989).

Breeding activity was clearly seasonal in *M. natalensis* and *T. leucogaster* in our study with breeding females (visibly pregnant or lactating) occurring in April and May. This is consistent with literature findings from populations of these or related species where reproductive activity appears to be linked in some way to the pattern of rainfall in areas which have well-defined wet and dry seasons. Breeding commences a few months after the onset of the rains and cease during the dry season (e.g. TAYLOR & GREEN, 1976; DELANY & MONRO, 1986; LEIRS et al., 1994; MONADJEM & PERRIN, 1997). In our study, the

peaks of pregnancies and lactations followed each other closely with a short time lag.

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REFERENCES

BEKELE, A. & H. LEIRS (1997). Population ecology of rodents of maize fields and grassland in central Ethiopia. *Belg. J. Zool.*, 127(1) : 39-48.

BEKELE, A., H. LEIRS & R. VERHAGEN (2003). Composition of rodents and damage estimates on maize farms at Ziway, Ethiopia. In : SINGLETON, G.R., L.A. HINDS, C.J. KREBS & D.M. SPRATT (eds), *Rats, mice and people : rodent biology and management*. ACIAR Monograph No.96. Canberra, Australian Centre for International Agricultural Research, pp. 262-263.

CHRISTENSEN, J.T. (1996). Home range and abundance of *Mastomys natalensis* (Smith, 1834) in habitats affected by cultivation. *Afr. J. Ecol.*, 34 : 298-311.

DELANY, M.J. & R.H. MONRO (1986). Population dynamics of *Arvicanthis niloticus* (Rodentia : Muridae) in Kenya. *J. Zool.*, 209 : 85-103.

FIEDLER, L.A. (1988). Rodent problems in eastern Africa. In : PRAKASH, I. (ed), *Rodent pest management*. CRC Press, Inc., Boca Raton, pp. 35-65.

FIEDLER, L.A. (1994). Rodent Pest Management in eastern Africa. FAO plant production and protection. *Bulletin* 123, Rome, Italy.

GOODYEAR, J.J. (1976). Population fluctuations of the rat-like rodents of importance in agricultural fields in Kaffa province, Ethiopia. *MA thesis*, Bowling Green State University pp. 72.

LEIRS, H., W. VERHEYEN, M. MICHIELS, R. VERHAGEN & J. STUYCK (1989). The relation between rainfall and the breeding season of *Mastomys natalensis* (Smith, 1834) in Morogoro, Tanzania. *Ann. Soc. Roy. Zool. Belg.*, 119 : 59-64.

LEIRS, H., R. VERHAGEN & W. VERHEYEN (1994). The basis of reproductive seasonality in *Mastomys* rats (Rodentia : Muridae) in Tanzania. *J. Trop. Ecol.*, 10 : 55-66.

LEIRS, H. (1995). *Population ecology of Mastomys natalensis (Smith, 1834). Implication for rodent control in Africa*. Belgian Administration for Development Co-operation, Agriculture Edition No. 35, 256pp.

LEIRS, H., R. VERHAGEN, W. VERHEYEN, P. MWANJABE & T. MBISE (1996). Forecasting rodent outbreaks in Africa : an ecological basis for *Mastomys* control in Tanzania. *J. Appl. Ecol.*, 33 : 937-943.

LEIRS, H., N. STENSETH, J.D. NICHOLS, J.E. HINES, R. VERHAGEN & W. VERHEYEN (1997). Stochastic seasonality and non-linear dependent factors regulate population size in an African rodent. *Nature,* 389 : 176-180.

LEIRS, H., R. VERHAGEN, C.A. SABUNI, P. MWANJABE & W. VERHEYEN (1997). Spatial dynamics of *Mastomys natalensis* in a field-fallow masaic in Tanzania. *Belg. J. Zool.*, 127(1) : 29-38.

LEIRS, H. (2003). Management of rodents in crops : the pied piper and his orchestra. In : SINGLETON, G.R., L.A. HINDS, C.J. KREBS & D.M. SPRATT (eds), *Rats, mice and people : rodent biology and management*. ACIAR Monograph No.96. Canberra, Australian Centre for International Agricultural Research, pp. 183-190.

MAKUNDI, R.H., T.J. MBISE, & B.S. KILOZO (1991). Observations on the role of rodents in crop losses in Tanzania and control strategies. *Beit. Trop. Land. Vet.*, 4 : 465-474.

MONADJEM, A. & M.R. PERRIN (1997). Population dynamics of *Lemniscomys rosalia* (Muridae : Rodentia) in a Swaziland grassland : effects of food and fire. *S. Afr. J. Zool.*, 32(4) : 129-135.

MWANJABE, P.S. (1993). The role of weeds on population dynamics of *Mastomys natalensis* in Chunya (Lake Rukwa) valley. In : MACHANG'U, R.S. (ed), *Economic importance and control of rodents in Tanzania*. Workshop proceedings, 6-8 July 1992. Morogoro, Sokoine University of Agriculture, pp. 34-42.

MWANJABE, P. & H. LEIRS (1997). An early warning system for IPM-based rodent control in small holder farming systems in Tanzania. *Belg. J. Zool.*, 127(1) : 49-58.

ODHIAMBO, C.O. & N.O. OGUGE (2003). Patterns of rodent pest distribution in a maize cropping system in the Kenyan Rift Valley. In : SINGLETON, G.R., L.A. HINDS, C.J. KREBS & D.M. SPRATT (eds), *Rats, mice and people : rodent biology and management*. ACIAR Monograph No.96. Canberra, Australian Centre for International Agricultural Research, pp. 217-219.

OGUGE, N.O., D. NDUNG'U & P. OKEMO (1997). Effects of neem plant (*Azadirachta indica* Juss, Maliaceae) products on maize grain consumption by three common rodent pests in Kenya. *Belg. J. Zool.*, 127(1) : 129-135.

TAYLOR, K.D. (1968). An outbreak of rats in agricultural areas of Kenya in 1962. *E. Afr. Agric. For. J.*, 34 : 66-77.

TAYLOR, K.D. & M.G. GREEN (1976). The influence of rainfall on diet and reproduction in four African rodent species. *J. Zool.*, 180 : 367-389.

TELFORD, S.R. Jr. (1989). Population biology of multimammate rat, *Praomys (Mastomys) natalensis* at Morogoro, Tanzania 1981-1985. *Bull. Fl. State Mus. Biol. Sc.*, 34(6) : 249-288.

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The role of rodents and small carnivores in plague endemicity in Tanzania

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ABSTRACT. Between 1974 and 2003, blood samples were collected from wild and commensal rodents, and wild and domestic small carnivores in selected villages of seven districts in Tanzania that have experienced human plague outbreaks and seven districts that have not experienced any outbreak of the disease. The samples were tested for antibodies against *Yersinia pestis* Fraction I antigen, using passive haemagglutination (PHA) or ELISA tests. Of the 3354 rodents and 558 small carnivores from the plague infected districts, 122 (3.6%) rodents (captured in Mbulu and Lushoto districts) were plague positive; 29 (5.2%) small carnivores from Mbulu, Arumeru, Hai and Lushoto districts were plague positive, 28 of these were domestic dogs (*Canis familiaris).* PCR tests showed that 17.5% of 211 rodents tested from Lushoto contained *Y. pestis* DNA. In the non-infected districts, 1545 rodents and 171 domestic dogs were tested. 11 (0.7%) of the rodents (captured in Monduli, Chunya and Masasi districts) were plague-positive. In Masasi district, 10.4% (7/67) of the rodents and 43.6% (17/39) of the dogs were positive for anti-*Y. pestis* IgG. It was concluded that wild and commensal rodents as well as wild and domestic small carnivores play a potential role as reservoirs and/or carriers of sylvatic plague in Tanzania, and that the disease exists in areas where human plague outbreaks have not occurred before. In order to update the distribution of the disease it is proposed that further epidemiological surveillance activities are established.

KEY WORDS : Rodents, small carnivores, plague, passive haemagglutination, ELISA. PCR.

INTRODUCTION

Plague has been endemic in Tanzania for more than a century. The first authentically recorded epidemic occurred at Image, Iringa in 1886. At the time of this outbreak, however, it was noted that the local people were quite familiar with the disease which was locally known as *"Chambafu/Shaambafu"* and that they knew it was associated with rodents. It was also noted that communities, under the guidance of their leaders, were burning houses as a means of controlling rodents and fleas and consequently controlling the disease (ROBERTS, 1935; MSANGI, 1968). The second authentically recorded epidemic occurred at Kiziba, Bukoba in 1897 (DAVIS et al., 1968). Likewise, the local people were already familiar with the disease that was referred to as **"***Rubunga***",** and were isolating plague patients as a means of controlling its spread. Based on available information, *Yersinia pestis* was isolated for the first time in Tanzania during this epidemic (DAVIS et al., 1968). The Kiziba focus is probably the oldest in the country as plague was introduced to this area from Uganda as far back as 1883 (CLYDE, 1962). Since then, the disease spread and established itself in many parts of the country especially the Central, North-eastern, Northern and South-western regions (Fig. 1). The spread was facilitated by slave and ivory caravans that mostly moved across the hinterland to the coast and through the Kilimanjaro region to Mombasa in Kenya. Indeed, most established plague foci today are found along the ancient slave and ivory trade routes (MSANGI, 1968; KILONZO, 1981).

Over the years, outbreaks of the disease have occurred in various parts of the country and involved large numbers of human cases and substantial case-fatality rates. During the past half century (1953 – 2003), a total of 8956 plague cases of whom 731 (8.2%) were fatal, were reported from ten districts in the country. Since 1980, however, only three districts (Lushoto, Singida and Karatu) have experienced outbreaks of the disease, and involved 8298 and 646 (7.8%) reported cases and deaths, respectively (KILONZO, 2003).

Prior to the studies reported in this paper, limited investigations were made to understand the species and ecology of rodents involved in the epidemiology of plague in the country. HUBBARD (1973) incriminated many rodent species in Tanzania as suitable reservoirs of plague in view of their hosting of flea species known to be efficient vectors of the disease elsewhere. Some observations made in plague – endemic areas in the country revealed that *Mastomys natalensis*, was the most frequent natural reservoir of plague and that it played an important role in maintaining the disease as it is partly refractory to the infection, and hence, it is not eradicated during plague epizootics (GUGGISBERG, 1966; HUBBARD, 1973). MSANGI (1968) demonstrated the presence of haemagglutination plague antibodies in 0.8% and 1.5% of clinically healthy *M. natalensis* and *Arvicanthis abyssinicus*, respectively. Many other wild rodent species including *Tatera robusta, Grammomys dolichurus; Rhabdomys pumilio* and *Otomys angoniensis* have been suggested as suitable reservoirs of the disease. This has been argued on the basis of seropositive assessments in Kenya where the ecological

and climatic features are similar to those in Tanzania, and the fact that these rodent species are abundant in areas where outbreaks of plague occur frequently and host similar flea species which are found on known rodent reservoirs (DAVIS et al., 1968; HUBBARD, 1973; SIONGOK et al., 1977).

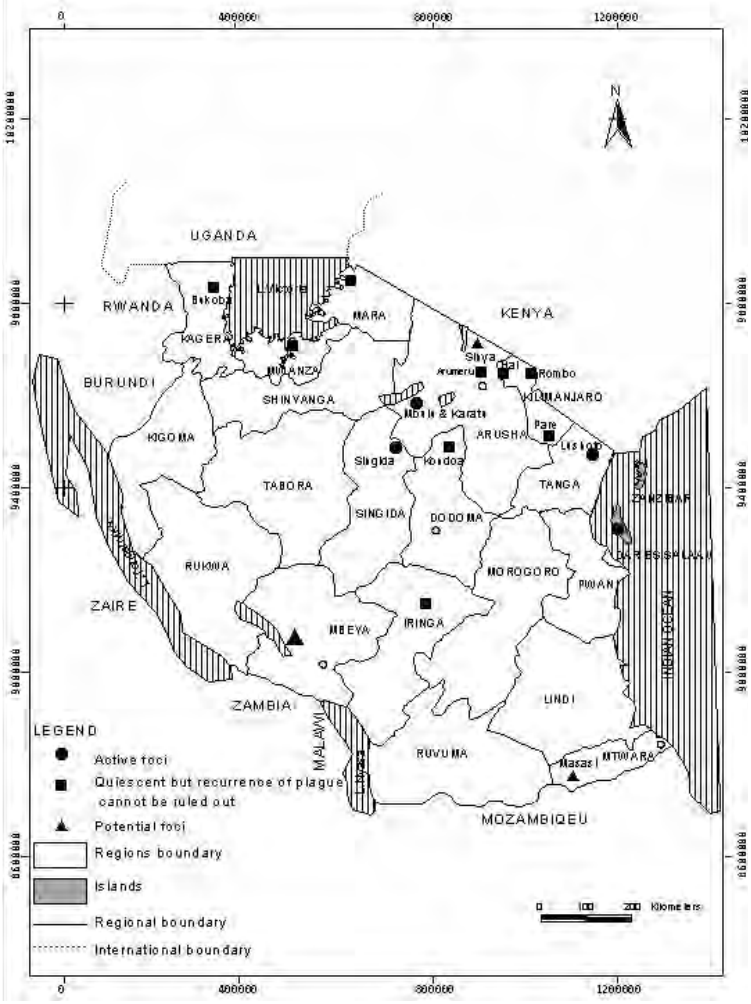

Fig. 1. – Distribution of plague in Tanzania (1953-2003).

Many outbreaks of human plague in the country have been associated with or preceded by large increases and/or mortalities of rodents in the infected area. The Wahehe people in Iringa, for example, reportedly observed that remarkable rat mortalities were associated with *"Chambafu"* (plague) outbreaks long before the arrival of German administrators in 1884 (MSANGI, 1968). LURZ (1913) similarly reported large numbers and deaths of rodent populations prior to the 1912 outbreak of plague in Rombo district. Likewise, the 1948 outbreak of the disease in Iramba district which involved 312 and 178 (57.1%) recorded cases and deaths, respectively, was preceded by large mortalities of rodents in late 1947 (ANONYMOUS, 1948). Similar population build-ups and plague epizootics were reported prior to plague outbreaks in Hanang (then Mbulu) and Same districts in 1951 and 1964, respectively (ANONYMOUS, 1951 and 1964). The first outbreak of human plague in Lushoto district in April, 1980 was preceded by large increases of rodent populations during the years 1978 – 1979 which prompted the use of zinc phosphide for their control in view of the severe damage caused to agricultural crops (MKAMI, 1980; KILONZO & MHINA, 1982).

The establishment of plague foci and distribution patterns in Tanzania has been based on outbreaks of the disease among human populations, rather than on substantiation of the disease among natural reservoirs in the particular area. In the past, very limited investigations were carried out to substantiate natural reservoirs, secondary reservoirs and/or carriers of the disease. In order to know its actual distribution, and hence be able to forecast outbreaks, adequate information on the reservoirs and carriers as well as its endemicity level and the population densities of its efficient vectors is desirable. The purpose of the present study was to partly fulfill this objective.

MATERIALS AND METHODS

Time and areas of study :

These studies were conducted at different times of the year, between 1974 and 2003. Seven districts that have experienced at least one recorded outbreak of human plague, and the same number of districts which have never recorded any outbreak of the disease, were selected for the study. The first category of districts (infected) comprised Singida, Mbulu, Arumeru, Hai, Rombo, Same and Lushoto. The second (un-infected) category of districts comprised Masasi, Chunya, Igunga, Monduli, Muheza, Kilombero and Morogoro-Rural (Fig. 2). At least two villages in each district were selected for the surveys. In plague-infected districts, the selected villages included the ones where the most recent outbreaks occurred.

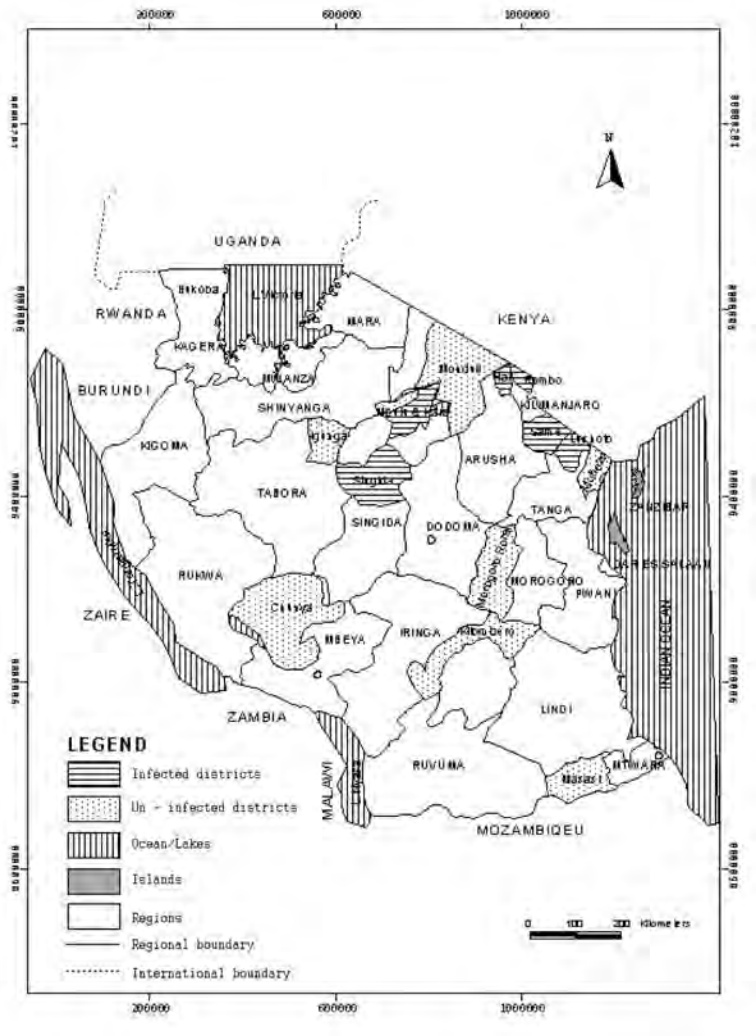

Fig. 2. – Areas surveyed for plague in Tanzania.

Trapping, collection and processing of specimens :

Sylvatic and commensal rodents were live-trapped using Sherman, Chauvancy or Box traps baited with peanut butter or roasted sardines. Traps were inspected in the morning with captures removed and taken to a central processing location. Live-captured animals were anaesthetized with ether and brushed with ether-soaked cotton wool to kill its arthropod ectoparasites which were then removed by scrubbing the fur of the animal with a small brush. Each animal was bled from the heart using a disposable syringe and needle or from the orbital vein using capillary tubes and capped microtubes. Flea ectoparasites were sorted, counted and preserved in 70% ethanol for their subsequent identification. Blood samples were left at room temperature overnight for spontaneous separation of serum with a minority of samples separated by centrifugation. Sera were preserved at 0-4ºC while in the field and at –20ºC after returning to the laboratory. In a few occasions, sera were preserved in liquid nitrogen.

In Hai, Rombo, Arumeru and Mbulu districts, small wild carnivores were live-captured with steel cage traps or killed by handgun. Venous blood was aseptically collected from the captured/shot animals and similarly processed. Collection and processing of blood from domestic dogs and cats was effected after obtaining informed consent from their owners.

Testing for plague infection :

A total of 4899 sera were tested against *Yersinia pestis* Fraction I (FI) antigen, using the Passive haemagglutination (PHA) test and controlled by the Passive haemagglutination inhibition (PHAI) test. Furthermore, 289 serum samples from Lushoto and Masasi districts were also tested by the Enzyme Linked Immunosorbent Assay (ELISA) and Polymerase Chain Reaction (PCR) techniques for detection of current and past infections.

RESULTS

A total of 3354 rodents were tested for anti-plague antibodies in the seven districts with established plague endemic foci. Of these, 122 (3.6%) were positive for specific haemagglutination antibodies against *Y. pestis* (Table 1a). Of the rodents tested in Lushoto district, 222 were also tested with the ELISA technique. Of these, 7.7% and 11.3% were positive for anti-plague IgG and IgM respectively (Table 1b). A total of 211 rodents from Lushoto were also subjected to PCR tests and 17.5% of them contained *Y. pestis* DNA (Table 1c). The seropositive rodents were captured in Mbulu and Lushoto districts, where recent and active human plague cases, respectively, have been recorded. A total of 1545 rodents were evaluated in the districts where outbreaks of the disease have not been reported. Of these animals, 15 (1.5%) were plague positive and had been captured in the Monduli, Chunya and Masasi districts (Table 2a).

A total of 729 small carnivores were examined from six plague-infected and two un-infected districts (Table 3). Of these, 47 (6.4%) were positive for plague antibodies. The majority (95.7%) of the positive carnivores were domestic dogs from the Arumeru, Mbulu, and Lushoto districts (plague-infected), and the Masasi district (uninfected). Other plague positive carnivores identified were one wild cat (*Felis lybica*) from the Hai district and one domestic cat (*Felis catus*) from the Masasi district (Table 3)..

TABLE 1a

Species and infection rates of rodents in districts with previous records of plague outbreaks :
(1a) Results of PHA tests

Rodent species tested	Nos. tested and (%) positive in each district							
	Singida	Mbulu	Arumeru	Hai	Rombo	Same	Lushoto	Total
Rattus rattus	96 (0)	37(8.1)	12 (0)	118 (0)	37 (0))	131 (0)	804 (3.4)	1235
Mastomys natalensis	355 (0)	43 (9.3)	78 (0)	19 (0)	84 (0)	35 (0)	552 (4.2)	1166
Arvicanthis nairobae	7 (0)	3 (0)	20 (0)	2 (0)	39 (0)	-	292 (2.2)	363
Lophuromys sp.	-	3 (0)	-	3 (0)	-	-	133 (6.8)	139
Pelomys fallax	-	-	-	-	-	-	60 (20)	60
Grammomys dolichurus	-	1 (0)	-	-	-	-	55 (3.7)	56
Otomys spp.	-	-	-	-	-	8 (0)	124 (11.3)	132
Heliosciurus sp.	-	-	-	-	-	-	17 (0)	17
Praomys spp.	-	-	-	-	-	-	3 (0)	3
Tatera robusta	21 (0)	-	3 (0)	-	8 (0)	16 (0)	3 (0)	51
Lemniscomys striatus	-	26 (11.5)	-	12 (0)	1 (0)	-	-	39
Rattus norvegicus	-	1 (0)	-	-	-	-	-	1
Cricetomys gambianus	-	-	-	9 (0)	28 (0)	-	1 (0)	38
Rhabdomys pumilio	-	-	35 (0)	-	4 (0)	-	-	39
Tachyoryctes daemon	-	-	1 (0)	-	2 (0)	-	-	3
Acomys spinossismus	-	-	-	-	-	8 (0)	-	8
Aethomys spp	4 (0)	-	-	-	-	-	-	4
Total	483 (0)	114 (8.3)	149 (0)	163 (0)	203 (0)	198 (0)	2044 (5.5)	3354 (3.6)

TABLE 1b

(1b) Results of ELISA tests on rodent sera from Lushoto district
(Range of titres :IgG : 1 :4 - 1 :128; IgM : 1 :8 - 1 :512; Minimum specific titre = 1 :4)

Rodent species	No. tested for antibodies	No. & % positive for IgG	No. & % positive for IgM
Mastomys natalensis	142	15 (10.6)	13 (9.2)
Arvicanthis nairobae	25	6 (23.1)	7 (26.9)
Lophuromys sp	14	1 (7.7)	2 (15.4)
Rattus rattus	19	2 (10.5)	2 (10.5)
Grammomys dolichurus	14	-	-
Praomys spp.	6	-	-
Mus (L) minutoides	1	-	-
Petrodromus sp.	1	1 (100)	1 (100)
Total	222	17 (7.7)	25 (11.3)

TABLE 1c

(1c) : *Yersinia pestis* DNA in rodents captured in Lushoto district :
results of Polymerase Chain Reaction (PCR) tests (Minimum specific titre =Lowest dilution of the test serum that produces positive reaction with specific Fraction I plague antigen).

Rodent species	Number tested	Number positive	% positive
Mastomys natalensis	131	25	19.1
Arvicanthis nairobae	25	7	28.0
Lophuromys sp	14	1	7.1
Rattus rattus	19	3	15.7
Grammomys dolichurus	14	0	0
Praomys sp.	6	0	0
Mus (Leggada) minutoides	1	0	0
Petrodromus sp. (Elephant shrew)	1	1	100
Total	211	37	17.5

TABLE 2a

(2a) Species, numbers and infection rates of rodents and insectivores tested in districts with no records of plague outbreaks. Figures in brackets refer to percentage of animals positive for plague. In Masasi, sera were tested by ELISA technique for detection of antibodies, in other districts PHA tests were used.

Animal species tested	Numbers tested and % infection in each district							
	Masasi	Chunya	Igunga	Monduli	Muheza	Kilombero	Morogoro Rural	Total
Rattus rattus	7 (0)	105 (2.9)	22 (0)	5 (0)	14 (0)	15 (0)	133 (0)	301
Mastomys natalensis	56 (12.5)	379 (0.8)	105 (0)	104 (1.9)	35 (0)	109 (0)	262 (0)	1050
Arvicanthis nairobae	-	6 (0	-	4 (0)	-	-	-	10
Aethomys sp.	2 (0)	-	-	-	-	-	-	2
Tatera robusta	2 (0)	17 (0)	-	7 (0)	6 (0)	-	1 (0)	33
Saccostomus campestris	-	2 (0)	-	-	-	-	-	2
Crocidura hirta	-	-	5 (0)	-	3 (0)	1 (0)	35 (0)	44
Lemniscomys griselda	-	-	-	-	-	-	3 (0)	3
Mus sp.	-	-	-	-	-	-	100 (0)	100
Total	67 (10.4)	509 (1.2)	132 (0)	120 (1.7)	58 (0)	125 (0)	534 (0)	1545 (1.5)

TABLE 2b

(2b) : Observation of Y. *pestis* F1 by ELISA tests of rodent sera collected in Masasi district

Species	No. tested for F1	No. & % positive for F1
Mastomys natalensis	45	14 (55.5)
Rattus rattus	7	1 (14.3)
Tatera sp.	2	0 (0)
Aethomys sp.	2	0 (0)
Total	56	15 (26.8)

DISCUSSION AND CONCLUSIONS

The present observations broadly indicated that many species of rodents are suitable and serve as natural reservoirs of plague in Tanzania. All these species could play an important role in the epidemiology of the disease. These observations are consistent with those reported from Kenya (DAVIS et al., 1968). As the examined rodents were clinically healthy when live-trapped, these animals are at least partly refractory, and hence, potentially capable of maintaining the disease enzootically for long periods. GUGGISBERG (1966) and HUBBARD (1973) suggested that *M. natalensis* was the major reservoir of the disease in Kenya and Tanzania and concluded that it was responsible for maintaining and passing the infection to the house rat, *R. rattus*, and to humans. Our observations are consistent with these reports; however, our data also indicated that other field rodent species including *Arvicanthis nairobae, Lemniscomys striatus, Lophuromys spp., Pelomys fallax, Grammomys dolichurus*, *Otomys* spp. and *Rattus rattus* could play similar roles in disease maintenance. Current studies in the Lushoto plague focus suggest close interaction and exchange of flea ectoparasites between sylvatic and commensal rodents, thus facilitating

TABLE 3

Species and infection rates of small carnivores in Tanzania. Dog sera from Masasi District were tested by ELISA technique.

Districts	Animal species examined and % infected								
	Canis familiaris	*Felis catus*	*Genetta genetta*	*Civettictis civetta*	*Crocuta crocuta*	*Felis lybica*	*Otocyon megalotis*	*Ichneumia albicauda*	Total
Arumeru	35 (11.4)	-	-	-	-	-	-	2 (0)	37 (10.8)
Hai	39 (0)	-	2 (0)	-	-	2 (50)	-	-	43 (2.3)
Rombo	-	-	-	1 (0)	-	-	-	1 (0)	2 (0)
Mbulu	55 (3.6)	-	-	-	2 (0)	2 (0)	3 (0)	-	62 (3.2)
Singida	19 (0)	-	-	-	-	-	-	-	19 (0)
Lushoto	388 (5.7)	7 (0)	-	-	-	-	-	-	395 (5.6)
Chunya	129 (0)	-	-	-	-	-	-	-	129 (0)
Masasi	39 (43.6)	3 (33.3)	-	-	-	-	-	-	42 (42.9)
Total	704 (6.4)	10 (10)	2 (0)	1 (0)	2 (0)	4 (25)	3 (0)	3 (0)	729 (6.4)

transfer of the disease causative agents (MAKUNDI et al., 2003).

Our observations further indicated that only two of the seven plague-active foci districts (Lushoto and Mbulu) demonstrated detectable haemagglutination antibodies. This was probably attributable to the fact that specimen collection in these districts was carried out during or soon after outbreaks of the disease, whereas in other districts the study was done several years after the occurrence of the last reported outbreak. These observations could suggest that the use of rodents alone is not enough for the detection of plague endemicity over long periods of time. The presence of both IgG and IgM immunoglobulins among rodent populations in Lushoto district was an indication of past and current infections but does not suggest how long ago the animals carrying IgG were infected.

Furthermore, our data showed that areas where outbreaks of human plague have not occurred before can also harbour animal reservoirs of the disease. Surveys in Monduli, Chunya and Masasi districts were carried out at times of epidemics of rodent populations, and where some rodent species were found to have been exposed to infection with *Y. pestis*. Considering the limited home range of the infected rodents, it is expected that the animals contracted the disease locally, thus suggesting the existence of endemic foci in these areas despite the absence of reported human plague outbreaks.

The presence of specific anti-plague antibodies and/or antigens in small carnivores (domestic dogs, domestic and wild cats) in districts where plague has occurred before (Arumeru, Mbulu, Lushoto and Hai) and in a district (Masasi) where the disease has not occurred before, suggests involvement of these animals in the epidemiology of plague in Tanzania as observed elsewhere (POLAND & BARNES, 1979; TAYLOR et al., 1981; ANONYMOUS, 1984). These animals are known to be efficient carriers of the disease and not more than 2% are killed by the pathogen (KARIMI, 1974 – Pers. Comm.). Anti-plague antibodies are also known to persist in small carnivores for long periods and the animals can occasionally serve as sources of human infection (RUST et al., 1971; BARNES, 1990).

Despite the low sampling and infection rates of carnivores, other than dogs, in our survey, the data suggest that such animals should, be involved in epidemiological studies aimed at establishing endemic foci of plague. Epidemiological surveillance services for plague should be established and regularly carried out in many districts; especially those, which experience frequent outbreaks of rodent populations. Such services will facilitate updating the distribution of natural foci of the disease in the country, the forecasting of outbreaks and allowing the prompt application of appropriate preventive measures. This improved information network will also enable researchers, extension personnel, community members and other people handling rodents in various parts of the country, to take the necessary precautions.

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REFERENCES

ANONYMOUS (1948). Annual Report of the Medical Department, 1948. *Government Printer, Dar es Salaam,* pg. 25.

ANONYMOUS (1951). Annual Report of the Medical Department, 1951. *Gouverment Printer, Dar es Salaam*, pg. 12-13.

ANONYMOUS (1964). Annual Report of the Medical Department, 1964. *Gouverment Printer, Dar es Salaam*, pg. 19.

ANONYMOUS (1984). Morbidity Weekly Report of 31 August, 1984. *Veterinary Plague* : Medicine Digest, 10 : 27.

BARNES, A.M. (1990). Plague in the United States of America : Present and Future. In : DAVIS,.L.R., R.E. MARSH; (eds). *Proceedings of the 14th Vertebrate Pest Conference*, 43-46.

CLYDE, D.F. (1962). Plague and Polio (1948-1956). In : History of the Medical Services of Tanganyika. *Government Press, Dar es Salaam,* 174-176.

DAVIS, D.H.S., R.B. HEISCH, D. MCNEILL & K.F. MEYER (1968). Serological survey of plague in rodents and other small mammals in Kenya. *Trans. Roy. Soc. Trop. Med. Hyg*., 62 : 838-861.

GUGGISBERG, C.A.W. (1966). Ecological studies of sylvan rodent plague reservoirs in Kenya. WHO Vector Control / 66.217, pg. 43. *Proceedings at the WHO Seminar on Rodents and Rodent Ectoparasites,* Geneva, October 1966.

HUBBARD, A.C. (1973). Observations on the life histories and behaviour of some small rodents from Tanzania. *Zool. Africana,* 7 : 419.

KILONZO, B.S. (1981). The origin, dissemination and present status of plague in Tanzania. *Dar. Med. Jour.*, 8 : 130-142.

KILONZO, B.S. & J.I.K. MHINA (1982). The first outbreak of human plague in Lushoto district, North-east Tanzania. *Trans. Roy. Soc. Trop. Med. Hyg*., 76 : 172-177.

KILONZO, B.S. (2003). The Ecology and Epidemiology of Plague in Africa, with special reference to Tanzania. *Proceedings of an International Workshop on the Epidemiology and Ecology of Q-fever, Tularemia and Plague.* Fogerty International Centre, National Institute of Health, Washington, USA.

LURZ, R. (1913). An epidemic of plague on Kilimanjaro in 1912. *Arch. Schiffs. Chd. Trop. Hyg*., 17 : 593-599.

MAKUNDI, R.H., B.S. KILONZO & A.P. MASSAWE (2003). Interaction between rodent species in agro-forestry habitats in the western Usambara Mountains, north-eastern Tanzania, and its potential for plague transmission to humans. In : SINGLETON, G.R., L.A. HINDS, C.J. KREBS & D.M. SPRATT (eds), *Rats, Mice and People*; Australian Centre for International Agricultural Research, Canberra : 20-24.

MKAMI, D.L. (1980). Taarifa ya Tauni tarehe 12/4/80 hadi 18/9/80, Lushoto. Unpublished report from the District Health Officer (Lushoto) to the District Medical Officer (Lushoto). Kumb. Na. HQ/41/LGC/176 of 24 August, 1980.

MSANGI, A.S. (1968). Observations on the endemicity of plague in Tanzania. *Ph.D. thesis,* University of London.

MSANGI, A.S. (1975). The surveillance of rodent populations in East Africa in relation to plague endemicity. *Dar es Salaam University Science Journal*, 1 : 8-15.

POLAND, J.D. & A.M. BARNES (1979). Plague. CRC Handbook series in zoonoses. STEELE, J.H. (ed), Inc. Boca Ralon, Florida, CRC Press.

ROBERTS, J.I. (1935). The endemicity of plague in East Africa. *E. Afr. Med. J.*, 12 : 200-219.

RUST, J.H., B.R. MILLER, M. BAHMANYAR, J.D, MARSHALL, JR PURNAVEJA, D.C. CAVANAUGH & S.T. HLA (1971). The role of domestic animals in the epidemiology of plague (iii). Antibody to *Yersinia pestis* in sera of dogs and cats. *J. Infect. Dis.*, 124 : 527-531.

SIONGOK, T.K.A., A.M. NJAGI & S. MASABA (1977) : Another focus of sylvatic plague in Kenya. *E. Afr. Med. J.*, 54 : 964.

TAYLOR, P., D.H. GORDON & M. ISAACSON (1981). The status of plague in Zimbabwe. *Ann. Trop. Med. Parasitol.*, 75 *:* 165-173.

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The population structure of four rodent species from a tropical region (Kisangani, D. R. Congo)

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ABSTRACT. This study summarizes the data on the population structure of *Deomys ferrugineus, Hybomys lunaris Lophuromys dudui* on the mainland and *Praomys jacksoni* on the mainland as well as on islands on the Congo River. All species at these three localities show a stable population structure without seasonal variation. Reproduction on the mainland populations is probably continuous year-round, with subadult presence during the whole year. The island populations of *P. jacksoni* have a different population structure from the mainland population, probably caused by the periodic inundations. The sex-ratio is even for *L. dudui* and *H. lunaris*. For *P. jacksoni* and *D. ferrugineus* however, more males were captured on the mainland. On the islands, the sex-ratio pattern is not clear cut and differs between years. No clear seasonal variation in sex-ratio has been found in our populations.

KEY WORDS : population structure, sex ratio, *Lophuromys*, *Praomys*, *Deomys*, *Hybomys.*

INTRODUCTION

Since 1979, the Faculty of Science, University of Kisangani conducts studies on Rodents in the region of Kisangani. During these studies, the structure of the rodent population and their ecological distribution was recorded. This work is a synthesis on existing data about the population structure of *H. lunaris, D. ferrugineus, L. dudui and P. jacksoni* from the region around Kisangani, from 1984 to 2000.

MATERIAL AND METHODS

Kisangani is located at 0°31' N, 25°11' E and lies between 360m and 460m above sea level. The area is situated in an equatorial climate type of the A_{fi} zone, according to the classification of Köppen (DUVIGNEAUD, 1974). The climate is characterized by the lack of a prolonged dry season. Precipitation is abundant with a monthly average of 152 mm, but rainfall is irregularly distributed. The mean relative humidity is 85% without much variation during the year. However, two short drier periods (December - February and June - August) and two wet periods (March - May and September - November) exist.

The survey is based on existing material collected from October 1984 to December 2000 from the city of Kisangani and its surroundings (Masako Forest Reserve and the islands Kungulu, Mbiye and Mafi on the Congo River). We used Victor snap traps and/or Sherman LFA live traps on line transects for our rodent trappings.

The results from October 1984 to December 1986 and 1997 are obtained at the Masako forest reserve on the mainland, except for *Lophuromys dudui*, where data from fallow lands near Kisangani city also exist and were pooled together with data from Masako. At Masako, 300 Victor snap traps have been used from 1984 to 1986 to totalize 13300 trap nights during a total of 27 months. The trapping effort was approximately evenly distributed during this period at Masako. In 1984, two months at the end of the wet season and one month of a 'drier' season were sampled. During 1997, 60 traps were used at Masako to totalize 780 trap nights. Sampling was only conducted during one wet season from September to November. In Kisangani city, 80 Victor traps were used with an unknown number of trap nights. Traps were baited with palm nut pulp (*Elaeis guineensis*), cassava, salty fish or peanut butter.

Mbiye and Mafi Islands were prospected together because of their vicinity. The study site was prospected in 1996 using 80 snap traps totalizing 2101 trap nights and again in 2000 using 83 Sherman live traps (2075 trap nights in total). At the Kungulu Island, 40 Sherman traps were used totalizing 960 trap nights in 1999. At all these localities, palm nut pulp was used as bait.

The trapping took place on transect lines with trap stations separated 10m from one another. The distance between the traplines varies between 500m to 1000m. We trapped across different habitats, including primary forests, secondary forests, fallow lands, periodically inundated secondary forests and along water courses. Within the city of Kisangani, we trapped in different types of fallow lands (older and younger fallow lands, concession of the university, …). The results from all habitats were pooled together since data on trap placement regarding to the habitat is not available.

The population structure is given for the two drier seasons and the two wetter seasons combined for the years 1985, 1986 and 2000. 1984 data represent part of the wet and one month of the 'drier' season (October – December). Data for 1997 and 1999 regarding to the seasons are not available.

Animals are categorized in groups based on reproductive characters as follows :

- Juvenile : females with non-perforated vagina and invisible teats or males with abdominal, non-developed testes
- Subadults : females with small visible nipples but a non-perforated vagina or males with non-scrotal testes (internally developed but not externally visible)
- Adults : females with large nipples and/or a perforated vagina or males with scrotal, externally visible testes

Body weight classes per age class were also calculated. Data were not available for the years 1984 and 1997. Data were grouped together per locality (for the years 1985 and 1986 at Masako). There was no variation in body weights between these two years (not shown).

The sex-ratio per year and combined over all years was calculated for each species at Masako on the mainland (except for 1997 and for the sampled months during 1984) and on the islands combined. Chi square tests were used to test for significant sex ratio bias within each species between years, as well as bias in the combined sex-ratio for all species over all years were data exist for the species. We expect an even sex ratio in small mammals (HARDY, 1997), but sex ratio bias have already been found in other small mammals (for instance for wild *Mus minutoides* individuals, KRACKOW, 1997) and linked to ecological factors, for instance in the rodent species *Mastomys natalensis* in Tanzania (KENNIS et al., submitted).

The material was fixated using 10% formaldehyde or 70% ethylic alcohol. The identification of the specimens was performed in the "Laboratoire d'Ecologie et de Gestion des Ressources Animales (LEGERA)" by comparing morphometric and craniometric data with those proposed by MEESTER & SETZER (1971), HOLLISTER (1916), HUTTERER & DUDU (1991), HUTTERER & HAPPOLD (1983).

RESULTS

Population structure in relation to the season

The population structure of *H lunaris, D. ferrugineus, L. dudui* and *P. jacksoni* in and around Kisangani is similar. In all species the population structure does not vary with the season (Figs 1-4), based on seasonal data from the years 1985, 1986, 1996 and 2000. For the years 1997 and 1999, information about the season of the captures is not available. Moreover, there were no records of *D. ferrugineus*, *H. lunaris*, and *L. dudui* in 1996, 1999 and 2000 at the prospected island sites, and only *P. jacksoni* was captured there.

The amount of subadults is larger than the amount of adults and juveniles from 1984 to 1986; except for *L. dudui*, where adults are more common. In 1997 however, adults seem dominant for our four study species. For *H. lunaris*, subadults are not represented in our trappings during this year. For the island populations surveyed during 1996, 1999 and 2000, *P. jacksoni* shows a high number of adults compared to subadults and juveniles. Total number of captures for each species and season is given in Table 1.

TABLE 1

Total number of captures per season (if available) for all species and years. DS = dry season, WS = wet season.

Year	84	DS85	WS85	DS86	WS86	97
H. lunaris	13	47	75	262	193	6
L. dudui	10	65	99	138	142	25
D. ferrugineus	19	50	89	127	105	34
P. jacksoni[1]	42	59	138	235	219	42
Year	DS96	WS96	99	DS00	WS00	
P. jacksoni[2]	43	80	28	72	61	

[1] data from Masako on the mainland
[2] data from the different islands on the Congo River

Figures

Fig. 1

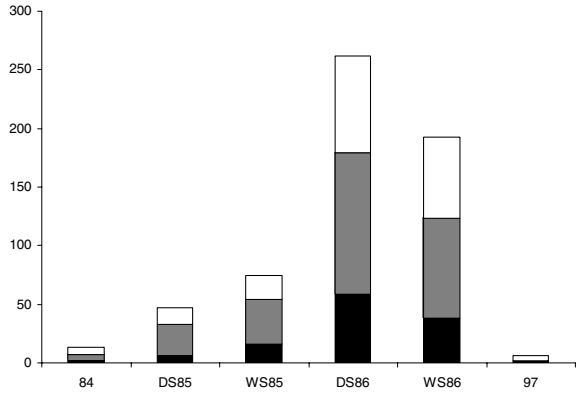

Fig. 2

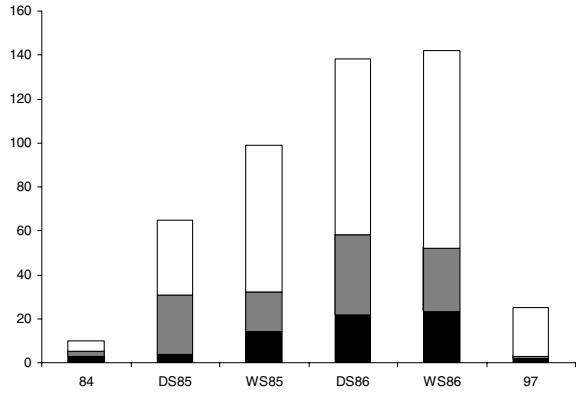

Fig. 1. – Population structure for *Hybomys lunaris*. Black = juvenile, shaded = subadult and white = adult. DS = dry season; WS = wet season. The Y-axis shows the number of captures.

Fig. 2. – Population structure for Lophuromys dudui. Black = juvenile, shaded = subadult and white = adult. DS = dry season; WS = wet season. The Y-axis shows the number of captures.

Fig. 3

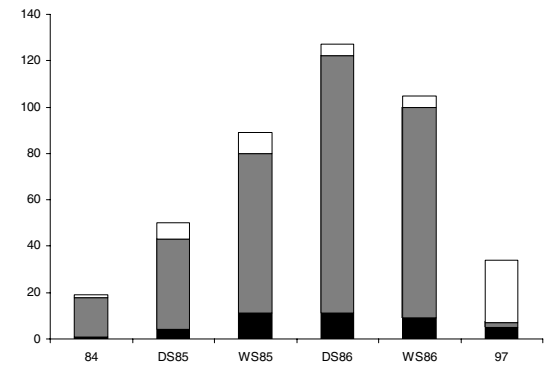

Fig. 4

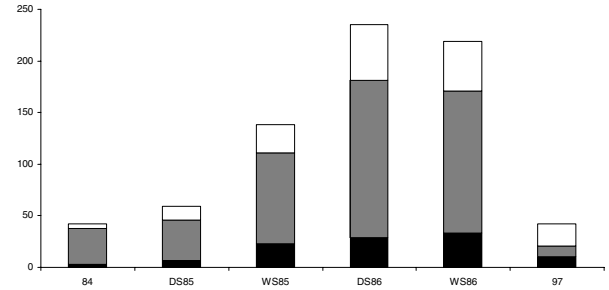

Fig. 5

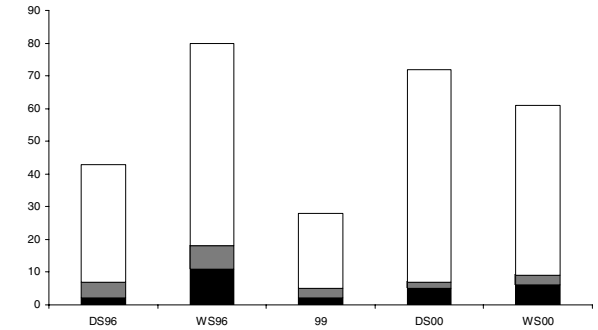

Fig. 3. – Population structure for *Deomys ferrugineus*. Black = juvenile, shaded= subadult and white = adult. DS = dry season; WS = wet season. The Y-axis shows the number of captures.

Fig. 4. – Population structure for the mainland populations of *Praomys jacksoni* (Masako, 1984-1986 and 1997). Black = juvenile, shaded = subadult and white = adult. DS = dry season; WS = wet season. The Y-axis shows the number of captures.

Fig. 5. – Population structure for the island populations of *Praomys jacksoni* (1996, 1999 and 2000). Black = juvenile, shaded = subadult and white = adult. DS = dry season; WS = wet season. The Y-axis shows the number of captures.

Age class composition

Body weight classes are given in Table 2. Upper limit of the body weight is given for juveniles and lower limit is given for adults. For subadults, ranges are given with outer bounds. The number of captures per age class is also indicated.

TABLE 2

Comparison between body weight W (in g) for all study species.Weight class data for 1884 and 1997 are not available. Data are grouped per locality. Lower limits are given for juveniles and upper limits are given for adults. For subadults, the range is given with outer bounds. Number of captures per weight class is given between brackets.

Year	85-86 W (g)	96 W (g)	99 W (g)	2000 W (g)
P. jacksoni				
Juveniles	<21 (91)	<22 (12)<23 (2)	<20 (8)	
Subadults	20-41 (423)	21-31 (11)	23-28 (3)	20-26 (10)
Adults	>40 (137)	>30 (100)	>29 (23)	>24 (117)
L. dudui				
Juveniles	<41 (89)			
Subadults	40-51 (240)			
Adults	>50 (115)			
D. ferrugineus				
Juveniles	<41 (33)			
Subadults	40-71 (312)			
Adults	>70 (26)			
H. lunaris				
Juveniles	<31 (116)			
Subadults	30-51 (271)			
Adults	>50 (190)			

Sex – ratio

Table 3 gives an overview of the sex-ratio calculations for the years 1985 and 1986 at Masako. *Lophuromys dudui* and *Hybomys lunaris* show an even sex-ratio year-round at Masako, without seasonal variation. For *Deomys ferrugineus* at Masako, the sex-ratio is significantly biased towards males in both the 'drier' and wet seasons ($X^2 = 5.5$, $p = 0.019$). When combining the data from 1985 and 1986, the overall sex-ratio is also significantly biased towards males ($X^2 = 11.4$, $p = 0.001$). For *Praomys jacksoni* on the mainland (Masako), the overall sex-ratio combined over the two study years is significantly biased towards males ($X^2 = 22.3$, $p < 0.001$). Only during the wet season of 1985, there was no significant difference in captures of males and females. All the other seasons during the two-year period show a sex-ratio which is significantly biased towards males ($X^2 > 6.1$, $p < 0.014$).

Data collected on the islands show a different sex-ratio pattern (Table 4). More males are caught than females during the wet seasons of 1996 ($\chi^2 = 5$, $p = 0.025$) and the 'edrier' seasons of 2000 ($\chi^2 = 4.76$, $p = 0.03$). However, during the wet seasons of 2000, a significantly female biased sex-ratio exists ($\chi^2 = 3.99$, $p = 0.047$). The overall sex-ratio, combined over all study years, does not show a significantly biased sex-ratio ($\chi^2 = 2.39$, $p = 0.12$) but shows a tendency towards more male captures (54.4% of total captures).

DISCUSSION

Age structure

The regular presence of all age classes on the mainland in and around Kisangani, indicates a stable population structure, even in the different seasons. Rodent reproduction is thus continuous in and around Kisangani. Only the year 1997 shows another pattern, but this is probably due

TABLE 3

Sex-ratio of *H. lunaris, L dudui, D. ferrugineus and P. jacksoni* collected at Masako during the years 1985 and 1986. Significant deviations from an equal sex-ratio are indicated with an asterisk. DS = dry season; WS = wet season.

	Total		**DS 85**		**WS 85**		**DS 86**		**WS 86**	
	N	**%**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**
H. lunaris										
Female	327	51.1	29	40.8	33	40.2	164	53.6	101	55.8
Male	313	48.9	42	59.2	49	59.8	142	46.4	80	44.2
Total	640		71		82		306		181	
χ^2	0.31		2,4		3,1		1,5		2,4	
L. dudui										
Female	107	44	9	40.9	23	43.4	40	47.6	35	41.7
Male	136	56	13	59.1	30	56.6	44	52.4	49	58.3
Total	243		22		53		84		84	
χ^2	3.46		0,7		0,9		0,2		2,3	
P. jacksoni										
Female	298	41	41	35	75	47.2	94	41.8	88	39.6
Male	425	59	76	65	84	52.8	131	58.2	134	60.4
Total	723		117		159		225		222	
χ^2	**22.3***		**10,5***		0,5		**6,1***		**9,5***	
D. ferrugineus										
Female	168	41.6	36	46.1	39	43.8	53	39.2	40	38.5
Male	236	58.4	42	53.9	50	56.2	80	60.8	64	61.5
Total	404		78		89		133		104	
χ^2	**11.4***		0,5		1,4		**5,5***		**5,5***	

TABLE 4

Sex-ratio of *Praomys jacksoni* captured on the islands. Significant deviations from an equal sex-ratio are indicated with an asterisk. DS = dry season; WS = wet season.

	Total		**DS96**		**WS96**		**99**		**DS00**		**WS00**	
	N	**%**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**
Female	139	45.6	30	47.6	30	37.5	12	42.8	22	36	45	61.6
Male	166	54.4	33	52.4	50	62.5	16	57.2	39	64	28	38.4
Total	305		63		80		28		61		73	
χ^2	2.39		0.14		**5.00***		0.57		**4.76***		**3.99***	

to the low trapping effort that year and the short period of trapping (3 months in one wet season) compared to the year-round trapping conducted at Masako during the other years reported here.

DIETERLEN (1986) found however that the age composition of rodents in primary forest changed significantly after reproduction. DUPLANTIER (1989) has also noted an influx of immature animals during the month of April for populations in tropical rainforest in Gabon, where the reproduction period extends from January to March. On the other hand, HAPPOLD (1974, 1979) found that the population structure of *Praomys tullbergi, Hylomyscus stella, Thamnomys rutillans, Lophuromys sikapusi* and *Graphiurus sp.* in the rainforest of Nigeria is composed of adults and subadults all year round, suggesting that the rodent populations there reproduce thus year-round. The continuous reproduction of rodents in and around Kisangani could be related to the absence of a real 'dry' season. We did not find any evidence to support the existence of well-defined reproductive periods in *L. dudui*, *P. jacksoni*, *D. ferrugineus* and *H. lunaris*.

In contrast to the rainforest, it is well known that most savannah species show distinct reproductive periods as documented by PIRLOT (1954) and DIETERLEN (1967) in Congo-Kinshasa, COETZEE (1965) in South Africa, SHEPPE (1972) and ANADU (1979) in Zambia, HUBERT (1977) in Senegal, NEAL (1977) in Uganda, LEIRS et al. (1989; 1990) in Tanzania. The population structure of savannah rodent populations thus changes considerably during the year.

Our data from the prospected islands show that the population structure of *Praomys jacksoni* on the islands differs from the population structure on the mainland. Although trapping effort and total number of individuals is lower on the islands than on the mainland, we think these results are real population effects because all the prospected years on the different islands show the same pattern. Adults form a much larger part of the population as opposed to the populations on the mainland (Masako and Kisangani). It is possible that these island populations have a different population structure because these islands are periodically inundated. The effect on the species composition is also clear, only the arboreal *P. jacksoni* was captured. During the inundation periods, animals have to find refuge in the trees. The arboreal *Praomys jacksoni* adults certainly can survive periodical, short inundation that last at most one week. Perhaps intraspecific competition for food during the inundations has an impact on the survival of juveniles and subadults or perhaps the juveniles (and maybe even subadults) have difficulties finding suitable trees to climb

in and find refuge. Perhaps there is a competition for 'good' trees with abundant food between adults and sub-adults/juveniles. Further studies are needed to clarify the causes of this population structure difference.

Sex -ratio

DUPLANTIER (1989) and HAPPOLD (1983) observed a male-biased sex-ratio for some Muridae and Cricetidae, similar to our observations for the mainland population of *P. jacksoni* and *D. ferrugineus*. Studies conducted by HAPPOLD (1977), CROSS (1977), RAHM (1967) have also found a preponderance of males for *Praomys jacksoni, Hylomyscus stella* and *Deomys ferrugineus*.

For *Hybomys lunaris* and *Lophuromys dudui* however, the sex-ratio is equal during the year.

For these species, similar results were also obtained by SHEPPE (1972; 1973), HAPPOLD (1977) and DUPLANTIER (1989).

The island populations of *Praomys jacksoni* show variations in sex-ratio depending on the season. This variation is different in our two different study years. During the wet season of 1996, more males were captured at the islands Mbiye and Mafi. In 2000 however, more females were captured during the wet season at island Kungulu. The populations on these islands are not stable and the periodic inundations can also have an effect on the sex-ratio. At the mainland, the sex-ratio does not show seasonal variation. These results could be influenced by the trapping efforts (although similar on the islands), by the different trapping methods and by differences in trappability between the sexes. Sex-specific differences in home ranges and dispersal can possibly influence the trappability of the different sexes. HUBERT (1977) found for instance that in savannas, rodent home ranges of males and females increase during the reproduction period. HAPPOLD (1983) noted that the home range of Muridae and Cricetidae varies from 100 to 300 m² and does not differ much according to the sex. DUPLANTIER (1989) however, found that the average home range of Muridae can measure more than 1500 m² for females whereas for males the home range could be even larger, especially in species like *Praomys tullbergi, Hybomys univittatus* and *Deomys ferrugineus*. He also found that the home range is inversely proportional to the density of the rodent population. If home ranges are larger for one sex, this can produce differences in trappability because of the higher mobility of one sex. Trappability can also be influenced by pregnancy and the care for offspring (by the females, males or both). No data on sex-specific trappability and sex-specific mobility exist but capture-mark-recapture studies and population genetic studies will be undertaken in the near future.

REFERENCES

ANADU, P.A. (1979). A study of bait selection in small African Rodents. *Acta Theriol.*, 24 : 501-511.

COETZEE, C.G. (1965). The breeding season of the multimmate mouse *Praomys (Mastomys) natalensis* (A. Smith) in the transvaal highveld. *Zool. Afri.*, 1(1) : 29-39.

CROSS, R.M. (1977). Population studies on *Praomys tullbergi* (Thomas) and other rats of forest regions of Sierra-Leone. *Rev. zool. Afri.*, 91(2) : 345-367.

DIETERLEN, F. (1967). La dynamique des populations de Muridés dans les forêts centrafricaines (Région du Kivu). *Chronique de l'IRSSAC*, 2 (2-3) : 33-34.

DIETERLEN, F. (1986). Seasonnal reproduction and population dynamics in Rodents of the African lowland rain forest. *Cimbebasia,* (A)8(1) : 1-7.

DUPLANTIER, J.M. (1989). Les Rongeurs myomorphes forestiers du Nord-Est du Gabon : Structure du peuplement, démographie, domaines vitaux. *Rev. Ecol.*, 44 : 329-346.

DUVIGNEAUD, P. (1974). La synthèse écologique : Populations, Communautés, Ecosystèmes, Biosphère, Noosphère. Ed. Doin, Paris VI, 286p.

HAPPOLD, D.C.D. (1974). The small Rodents of Forest-savannah-farmland association near Ibadan, Nigeria, with observation on reproduction biology. *Rev. Zool. Afr.*, 88(4) : 814–836.

HAPPOLD, D.C.D. (1977). A population study on small rodents in the tropical rain forest of Nigeria. *Terre & Vie*, 31 : 285-458.

HAPPOLD, D.C.D. (1979). Age structure of a population of *Praomys tullbergi* (Muridae, Rodentia) in Nigeran rain forests. *Terre & Vie*, 33 : 253-274.

HAPPOLD, D.C.D. (1983). Rodents and Lagomorphs. *Trop.Savanas*, 16 : 363-400.

HARDY, I.C.W. (1997). Possible factors influencing vertebrate sex ratios : an introductory overview. *Applied Animal Behaviour Science*, 51 : 217-241.

HOLLISTER, N. (1916). Shrews collected by the Congo Expedition of The American Museum. *Bull. Amer. Mus. Nat. Hist.*, 35 : 663-680

HUBERT, B. (1977). Ecologie des populations de Rongeurs de Bandia (Sénégal), en zone

Sahelo-Soudanniene. *Terre & Vie,* 31 : 33-100.

HUTTERER, R. & A.M. DUDU (1991). Redescription of *Crocidura caliginea*, a rare shrew from northeastern Zaïre (Mammalia, Soricidae). *J. Afr. Zool.,* 104 : 305-311.

HUTTERER, R. & D.C.D. HAPPOLD (1983). The Shrews of Nigeria, genus *Sylvisorex* from Rwanda and Zaïre (Insectivora, Soricidae). *Z. Säugetierk.*, 50 : 266-271.

KRACKOW, S. (1997). Maternal investment, sex-differential prospects, and the sex ratio in wild house mice, *Behav. Ecol. Sociobiol.*, 41 : 435-443.

LEIRS, H., W. VERHEYEN, M. MICHIELS, R. VERHAGEN & J. STUYCK (1989). The relation between rainfall and the breeding season of *Mastomys natalensis* (Smith, 1834) in Morogoro, Tanzania, *Ann. Soc. r. Zool. Belg.*, 119 (1) : 59-61.

LEIRS, H., J. STUYCK, R. VERHAGEN, W. VERHEYEN (1990). Seasonal variation in growth of *Mastomys natalensis* (Rodentia, Muridae) in Morogoro, Tanzania. *Afr. J Ecol.*, 28 : 325-341.

MEESTER, J. & H.W. SETZER (1971). The Mammals of Africa : an Identification Manual. Smithsonian Institution Press Washington.

NEAL, B.R. (1977). Reproduction of the multimammate rat *Praomys (Mastomys) natalensis* (Smith) in Uganda. *Z. Säugetierk.*, 42 : 221-231.

PIRLOT, P.L. (1954). Pourcentage de jeunes et périodes de reproduction chez quelques rongeurs du Congo Belge. *Ann. Mus. Congo*, Tervuren, Zool. 1 : 41-46.

RAHM, U. (1967). Les Muridées des environs du lac Kivu et des régions voisines de l'Afrique centrale et leur écologie. *Rev. Suisse Zool.*, 74 : 439-520.

SHEPPE, W.A. (1972). The annual cycle of small mammal populations of a Zambian floodplain. *J. Mamm.*, 53 (3) : 445-460.

SHEPPE, W.A. (1973). Notes on Zambian Rodents and Shrews. *Puku,* 7 : 167-190.

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Preliminary data on the biodiversity of rodents and insectivores (Mammalia) in the periphery of Kisangani (D. R. Congo)

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ABSTRACT. This study presents the species diversity of rodents and insectivores s.l. as observed in the forests around Kisangani (D.R. Congo) between 1979 and 2003. 7736 specimens were collected using Victor snap traps, Sherman live traps and pitfalls. In total, 49 small mammals species (36 rodents and 18 shrews) were identified of which 42 were actually captured and 7 more were observed around Kisangani.

The number of species varied between habitats : 16 species were found (12 rodents, 4 shrews) in primary forest, 36 species (21 rodents, 15 shrews) in secondary forest, 31 species (20 rodents, 11 shrews) in fallow lands and 16 species (15 rodents and 1 shrew) in wetlands. On the right bank of the Congo River, 40 species were collected against 19 on the islands and 15 on the left bank of the Congo River. At this stage, the right bank seems to be more diverse as far as the small mammal fauna is concerned, but more studies on the left bank need to be conducted.

KEY WORDS : biodiversity, Rodentia, Insectivora, Kisangani, Democratic Republic of Congo.

INTRODUCTION

In the Democratic Republic of Congo, small mammal phylogeny and zoogeography are thoroughly studied in the eastern national parks and their peripheral zones, with syntheses by HOLLISTER (1916), HATT (1940) and SCHOUTEDEN (1948).

Ecological studies of small mammals in the Democratic Republic of the Congo (DRC) forest zones are rare however. According to COLYN (1986), most of the rain forest region between the Congo River and the Rift Valley, although recognized as containing some endemic species, remains unstudied. DUDU (1991) also noted that the small mammal species from eastern Kivu (Albertine Rift) was studied much better than that of other regions of the DRC, more particularly the lowland rainforests.

In Kisangani, small mammal studies (shrews and rodents) started in 1979 in order to determine their specific diversity and ecology. Some results were already published by DUDU et al. (1985, 1997, 2005); COLYN & DUDU (1986); DUDU & GEVAERTS (1986, 1987); DUDU (1989), HUTTERER & DUDU (1990); KADANGE et al. (1998). Data on other collections are still unpublished, for instance the shrew collections of which specimens remain to a large extent unidentified.

This work is a synthesis of the main results from the study on the diversity of small mammals around Kisangani in different types of forests and the derived, anthropogenic habitats. We will establish the specific richness and distribution of rodents and shrews in all habitats by combining the available data from 1979 to February 2003.

MATERIAL AND METHODS

Study areas

The forest zones studied lie within a radius of about 50 km around the city of Kisangani (0°31'N, 25° 11'E, altitude 396-425 m above sea level). Previously covered by primary rainforest, this area contains at present different forest ecosystems (primary and secondary forests) on the two banks of the Congo River and its islands and is also characterised by peri-urban degraded areas (fallow lands and fields). It includes localities that, according to the distribution stated by COLYN (1991), are part of the East Central faunistic zones (islands and right bank of the Congo River) and South Central faunistic zone (left bank).

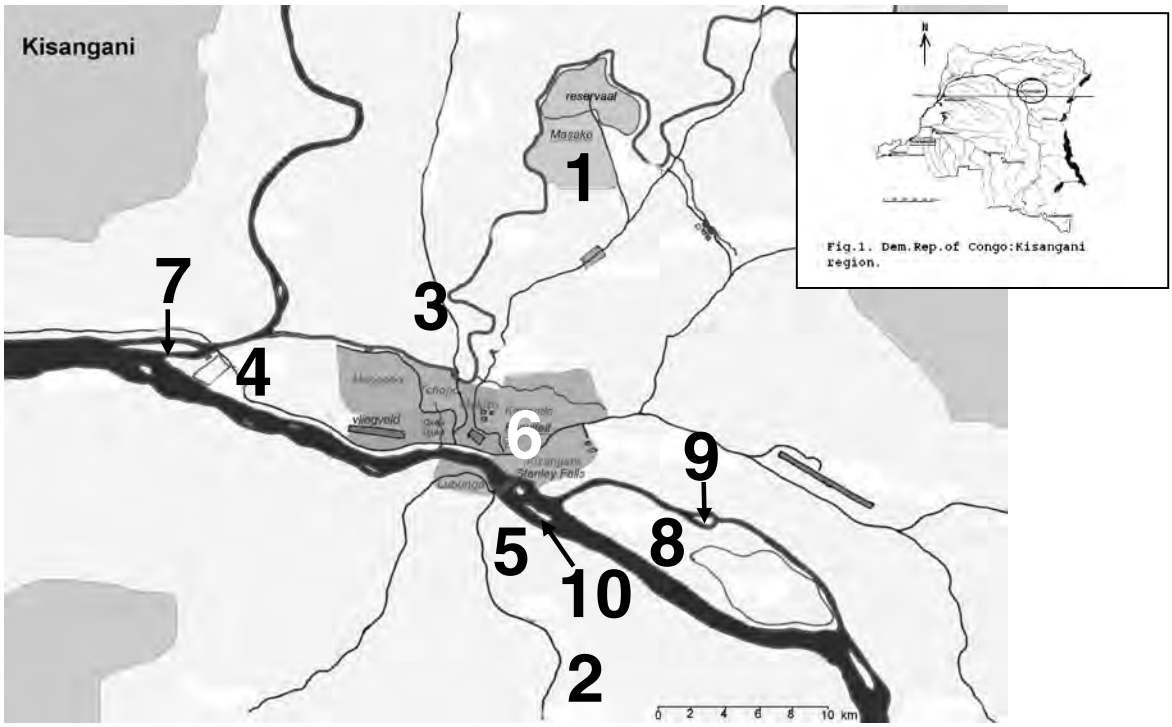

Fig. 1. – Map of the Kisangani area (after H. Gevaerts) indicating the different study sites. 1 : Masako forest reserve; 2 : Yoko forest reserve; 3 : Zoo Kisangani; 4 : Linoko; 5 : Lula; 6 : Kisangani town; 7 : Kungulu island; 8 : Mbiye island; 9 : Mafi island; 10 : Tundulu island. Inlay : map of D.R. Congo showing the position of Kisangani.

The main study sites (Fig. 1) are the protected areas (Masako, Yoko, forest of the Kisangani Zoo), islands within the Congo River (Mbiye, Mafi, Kungulu and Tundulu) and the surroundings of Kisangani city (Kabondo, Grand-seminaire, Linoko, concession of the Science Faculty, Plateau medical, Plateau Boyoma, Kikongo and finally Lula on the left bank of the Congo River).

Masako Forest Reserve (2.105 ha) is located 15 Km north-east of Kisangani, on the old Buta's road. One third of the reserve is occupied by primary forest; the remainder consists of old-growth secondary forests, fallow lands and crops. The Yoko Forest Reserve (6.975 ha) lies south of Kisangani, on the left bank of Congo River, between 21 and 38 km, towards Ubundu. It consists of young and old-growth secondary forests. The Zoo of Kisangani (84 ha), an artificial forest, is located on the right bank of Tshopo river, 4 km from the city, on the road towards Buta. The islands Mbiye (5600 ha), Tundulu (76 ha) and Mafi (20 ha) are located upstream on the Congo River to the south-east of Kisangani. Only Kungulu island (100 ha), at the convergence of the Lindi and the Congo rivers, lies downstream from Kisangani city. All islands are covered by primary forests, secondary forests, fallow lands and wetland forests.

Primary forest :

This type of habitat is essentially composed of *Gilbertiodendron dewevre*i and *Scaphopethalum thonneri* as undergrowth, whereas for the wetter areas on the different islands, it is heterogeneous and semi deciduous with *Gilbertiodendron dewevrei* and *Coelocaryon bothryoides* on Mbiye and *Piptadeniastrum africanum* and *Celstis mildbraedtii* on Kungulu. The undergrowth is dominated by *Cyathogyna viridis* and *Pycnocoma insularis* respectively on Mbiye and Kungulu islands (MOSANGO, 1991; NSHIMBA, unpublished data).

Secondary forest :

The secondary forests are very diverse, comprised of a mixture of trees also occurring in old fallow lands and primary forest. On the right bank of the river, it is characterised by *Zanthoxylum gilletii, Cynometra hankei, Peterstiantus macrocarpus, Musanga cecropioides, Terminalia superba,* etc., and on the left bank by *Scorodophloeus zenkeri, Albizia adiantifolia, Uapaca guineensis, Cynometra alexandrii, Panda oleoza, Musanga cecropioides,* etc. (LOMBA & NDJELE, 1998)

Wetland forest :

The wetland forests are constantly or periodically inundated and this habitat is composed out of various trees depending on whether they are located in the forest or on banks of watercourses. They include : *Uapaca guineensis, Uapaca heudolotii, Mitragyna stipulosa, Trichilia retusa, Coelocaryon botryoides, Alchornea cordifolia, Costus lucanisianus,* etc.

Fallow lands :

Formed essentially by herbaceous groupings consisting of *Panicum maximum*, *Pennisetum purpureum*, *P. polystachyon*, *Spermacoce latifolia* and of shrub associations of *Cnestis ferruginea*, *Craterispemum cerinanthum*, *Afromomum laurentii* and *Costus lucanisianus*, *Triumpheta cordifolia* and *Selaginella myosurus*. (NYAKABWA, 1982 and BAELONGANDI, unpublished data)

Kisangani region within the equatorial climate zone of the Afi type according to the Köppen classification. Precipitation is abundant year-round but not uniformly distributed, with a monthly average around 152mm (1970-1990). Even during the driest month there is more than 60mm rainfall and a relative humidity averaging 85%. Therefore there is no real dry season, but two 'drier' seasons with weak precipitation exist : December - February and June-August with a minimum in January. Two wet seasons exist with heavy precipitation : March-May and September-November with maxima in April and in October.

Capture-removal studies were carried out in different biotopes with the use of various trapping techniques, such as pitfalls, capture-removal grids and capture-removal lines with different trap systems. Mostly the sampling was conducted during one-year periods, with captures each month. The sample years were not always consecutive. In rare cases, the sampling period was shorter (3 to 6 months). Specimens were sampled using removal trapping in lines and in grids, with Victor Rat traps (175 x 85 mm) and Sherman LFA live traps (76 x 89 x 229 mm), both baited with palm nut, cassava bread or cassava carrot. Traps were placed at 10m distance; the distance between the lines varied from 500 to 1000m. The number of traps and the length of the trapping line varied according to the dimensions of the different habitats and the study aspects. Grids have only been used at Masako from 1985 to 1988. Twelve grids were used in fallow lands, 12 grids in the secondary forest and 4 in the primary forest. The grids (100 x 100m) consisted of 100 signposted trap stations, placed at 10m distance, with two traps per station within a radius of 1m from the signpost. A grid was thus covered by 200 traps and the grids were separated by minimum 200m distance.

Since November 2001, the pitfall capture technique permitted to increase the specific richness of rodents and shrews of certain localities. Each pitfall line had a length of 105 m with a station each 5 metres, thus the pitfall line consisted of 20 plastic buckets, buried so that the rim was level with the ground. The buckets were 290 mm high with a superior diameter of 290 mm and a lower diameter of 220 mm. The bottom was pierced with small holes to permit the infiltration of water during rain showers. The pitfalls were installed following protocols in STANLEY et al. (1998) and NICOLAS et al. (2003). A canvas or plastic drift fence of 0.5m height was constructed that bisected the rim of the buckets. At each end of the pitfall line, the fence was prolonged for 2.5 metres beyond the last bucket. Generally, we constructed three pitfall lines within different habitats at each locality. The distance between two lines varied according to the explored localities : from 200m to 2000m for Masako and from 300 to 1000m for the islands (Mbiye and Kungulu). The trapping continued for 3 to 6 days (Victor and Sherman traps) or for 21 consecutive days (pitfall lines) during a sampling period that varied from 1 to 12 months per study year.

Sampling periods per locality are as follows :

Kungulu :
December 1978 to April 1979;
May – August 1998;
February, March and July 1999;
February 2003.

Tundulu :
December 1980 to April 1981;
May to July 1994

Mbiye :
October 1982;
December 1994 to September 1996;
January to December 2000
February 2002.

Kisangani city :
August 1993 to July 1994;
August to November 1997;
June 1998 to February 1999;
May 1994 to August 1994

Zoo :
January to June 1980;
June 1985 to May 1986;
December1995 to October 1996

Yoko :
June 1995 to May 1996

Masako :
October 1984 to November 1985;
December 1985 to December 1986;
April 1985 to April 1986;
June 1986 to April 1988;
May 1996;
September 1997 to November 1997;
June 1999 and November 2001.

The specimens were fixed in formalin 10% and biopsies were preserved in ethylic alcohol 85%. The determination of rodents was effected at first at the University of Antwerp, Belgium (Evolutionary Biology Group, late Prof. Verheyen) then later at the Laboratoire d'Ecologie et de Gestion des Ressources Animales (LEGERA, Kisangani) by comparing morphometric and cranio-dental characters as described by DELANY (1975), HOLLISTER (1916), MEESTER & SETZER (1971), HUTTERER & HAPPOLD (1983), HUTTERER & DUDU (1990). Shrew specimens were identified at the Alexander Koenig Museum (Germany) and the University of Rennes (France) with morphological (skull morphometrics) and karyological techniques.

We calculated different indices of diversity for the different study localities and habitats. We calculated the Shannon –Wiener diversity index using the following formula :

$H = -\Sigma(pi \log_2 pi)$ (BARBAULT, 1981).

We also calculated the equitability E using the formula H/Hmax and the Simpson's index

$D = 1 - \Sigma(pi)^2$.

Finally, we calculated the trapping success (the number of individuals captured per 100 trap nights).

RESULTS

The materiel collected sums up to 7736 specimens (rodents and insectivores combined), with in total 25 species of rodents (4 families) and 17 species of shrews or

TABLE 1

Diversity indices for the Rodentia and Insectivora captured at all mainland study sites, per habitat and per study site. Masako, the zoo and Kisangani town lie on the right bank of the Congo River, Yoko and Lula are situated on the left bank. The number of specimens is indicated, together with the specific richness SR (number of species), the Shannon-Wiener Index H, the equitability E and the Simpson Index. PF = primary forest, SF = secondary forest, FL = fallow land, WF = wetland forest, total = total per study site, if more than one habitat was prospected.

	Masako					Zookis.				Ki. Town	Yoko				Lula
	PF	SF	FL	WF	Total	SF	FL	WF	Total	FL	SF	FL	WF	Total	FL
Rodentia															
# spec.	168	1809	1772	410	4159	274	157	44	475	766	64	54	73	191	100
SR	12	19	19	15	23	6	9	6	11	10	7	9	7	12	8
H	2.18	2.75	3.04	3.04	3.06	1.62	2.03	0.51	2.04	1.74	1.63	2.73	2.17	2.34	2.29
E	0.61	0.65	0.71	0.78	0.68	0.63	0.64	0.20	0.59	0.52	0.58	0.86	0.77	0.65	0.77
Simpson	0.87	0.80	0.85	0.85	0.84	0.60	0.61	0.99	0.66	0.54	0.57	0.81	0.71	0.63	0.76
Insectivora															
# spec.	24	78	39	9	150					35	3	7	10	20	3
SR	4	15	10	4	16					4	2	1	1	2	2
H	1.52	2.93	2.90	1.01	2.96					0.79	0.92			0.29	0.92
E	0.76	0.75	0.87	0.51	0.74					0.39				0.29	
Simpson	0.60	0.81	0.84	0.34	0.82					0.26	0.44			0.10	0.44

TABLE 2

Diversity indices for the Rodentia and Insectivora captured at all island study sites, per habitat and per study site. The number of specimens is indicated, together with the specific richness RS (number of species), the Shannon-Wiener Index H, the equitability E and the Simpson Index. PF = primary forest, SF = secondary forest, FL = fallow land, WF = wetland forest, total = total per study site, if more than one habitat was prospected.

	Mbiye					Kungulu				Tundulu			Mafi
	PF	SF	FL	WF	Total	PF	SF	FL	Total	SF	FL	Total	FL
Rodentia													
# capt.	305	223	298	298	1124	36	100	72	208	86	104	190	83
SR	6	8	9	6	11	4	8	7	10	2	3	4	8
H	0.84	0.87	1.19	1.21	1.58	1.88	2.04	2.44	2.39	0.09	0.95	0.69	1.96
E	0.32	0.29	0.38	0.47	0.34	0.94	0.68	0.87	0.72	0.09	0.60	0.35	0.65
Simpson	0.26	0.25	0.36	0.42	0.33	0.71	0.70	0.79	0.75	0.02	0.38	0.24	0.62
Insectivora													
# capt.	67	12	44	29	152	9	45	6	60				20
SR	3	1	2	2	4	1	4	1	4				1
H	1.04		0.77	0.41	0.87		0.86		0.66				
E	0.66		0.77	0.41	0.44		0.43		0.33				
Simpson	0.48		0.35	0.98	0.37		0.31		0.22				

TABLE 3

Total number of species, trap nights, number of specimens and trap success per locality (rodents and insectivores combined). * Total number of trap nights not available.

	Masako	Zookis	Kisangani	Yoko	Lula	Mbiye	Kungulu	Tundulu	Mafi
# Species	39	11	14	14	10	15	14	4	9
Trap nights	19465	2212	2994	2880	670	9756	3016	750	*
Total # captures	4309	475	801	211	103	1276	268	190	103
Trap success	22.14	21.47	26.75	7.33	15.37	13.08	8.89	25.33	*

elephant shrews (3 families). The following Rodentia were found : *Colomys goslingi, Dendromus mystacalis*, *Deomys ferrugineus, Funisciurus.pyrrhopus, Funisciurus anerytrus, Grammomys kuru, Graphiurus lorraineus, Graphiurus surdus, Hybomys lunaris, Hylomsycus stella, Hylomyscus aeta, Hylomyscus parvus, Lophuromys dudui, Lophuromys flavopunctatus, Lemniscomys striatus, Malacomys longipes, Mastomys natalensis, Mus minutoides, Oenomys hypoxanthus, Praomys jacksoni, Praomys mutoni, Praomys misonnei, Paraxerus boehmi, Rattus rattus* and *Stochomys longicaudatus.*

The following Insectivora (sensu lato, including Chrysochloridae and Macroscelidae) were found : *Amblysomys leucorhinus, Crocidura olivieri, C. cfr. hildegardeae, C. denti, C. dolichura, C. jacksoni, C. latona, C. littoralis, C. cfr. ludia, C. congobelgica, C. caliginea, Petrodromus tetradactylus, Rynchoncyon cirnei, Scutisorex somereni, Sylvisorex jonhstoni, Sylvisorex cf oriundus* and *Suncus infinitesimus*.

TABLE 4

Trap nights, number of specimens and trapping success per habitat for the localities and years were these data are available. Several years were thus omitted. The year 2001 at Masako was omitted here due to unfinished determination work. PF = primary forest, SF = secondary forest, FL = fallow land, WH = wet habitat.

	Masako (1985-1987, 1997, 1999)				Mbiye island (1996, 2000, 2002)				Kungulu island (1999, 2003)		
	PF	SF	FL	WH	PF	SF	FL	WH	PF	SF	FL
# captures	141	1705	1691	362	220	109	223	171	32	198	25
Trap nights	830	6480	5790	1480	1936	1060	2141	2168	280	2280	200
Trap. success/hab.	16.99	26.31	29.21	24.46	11.36	10.28	10.42	7.89	11.43	8.68	12.50

Eight other species were not captured but often observed in the wild or found at game meat markets and are thus added to the species list : *Anomalurus beecrofti* and *A.derbianus* (Anomaluridae), *Protoxerus stangeri* and *Heliosciurus rufobrachium* (Sciuridae), *Atherurus africanus* (Histricidae), *Thryonomys swinderianus* (Thryonomidae), *Cricetomys emini* (Cricetidae) and *Potamogale velox* (Potamogalidae).

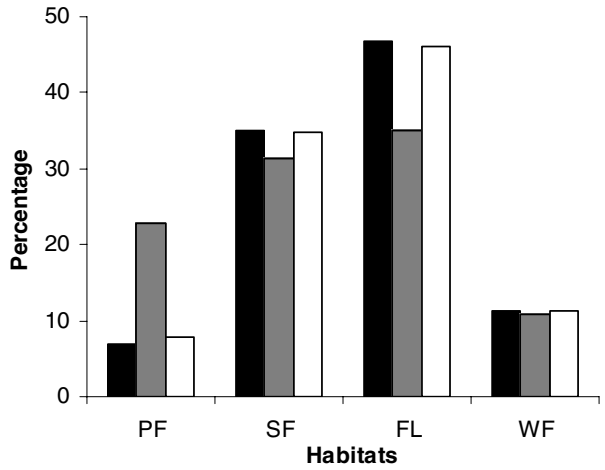

Fig. 2. – Total number of captures per habitat for rodents (black), insectivores (shaded) and rodents and insectivores combined (white).

In total, 99% of captures were rodents. Masako yielded the highest diversity (H=3.06, E=0.68, D=0.84 for rodents and H=2.96, E=0.74, D=0.82 for shrews), as indicated by Tables 1 and 2. The highest trapping success was observed in degraded areas (in town and on Tundulu island); the lowest trap success values were found at the Yoko reserve (7.33%) and the island Kungulu (8.89%), as indicated by Table 3. Trap success per habitat is given in Table 4 for all localities where these data are available.

The most common species captured during our study in the different habitats are *Praomys jacksoni, Lophuromys dudui* and *Lemniscomys striatus*. *Praomys jacksoni, Lemniscomys striatus, Hylomyscus stella, Hybomys lunaris, Oenomys hypoxanthus, Mus minotoïdes, Stochomys longicaudatus, Gramnomys kuru (*formerly *Thamnomys rutilans), Rattus rattus, Malacomys longipes* and *Lophuromys dudui* occur almost everywhere. A few species are particular to one bank of the Congo River. *Praomys misonnei, P. mutoni, Hylomyscus aeta, Hylomyscus parvus, Paraxerus boehmi, Funisciurus pyrrhopus, Deomys ferrugineus* and *Dendromys mysticalis* appear to be strictly confined to forests of the right bank of the Congo River. In contrast, *Lophuromys flavopunctatus* occurs abundantly on the left bank of the Congo River in forests as well as in fallow lands. The highest diversity is recorded on the right bank with 40 species of which Masako alone is populated by 39 species and represents 55.7% of all captures. On the islands, 19 species (14 rodents, 5 shrews) are present and on the left bank, although few studies have taken place there, 15 species are present (12 rodents, 3 insectivores).The specific diversity varies in the different habitats. In the forests (primary and secondary), 45 species (38 captured and 7 observed, 30 rodents and 15 insectivores) are found, against 38 species in fallow land (31 captured and 7 observed, 26 rodents and 12 insectivores).

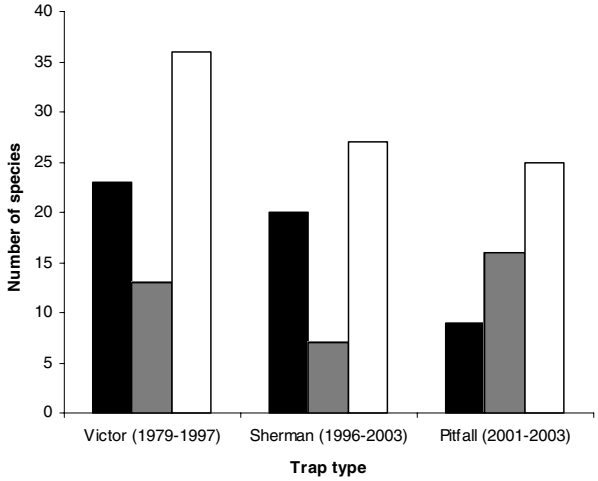

Fig. 3. – Number of species per trap type for rodents (black), insectivores (shaded) and rodents and insectivores combined (white).

Species distribution differs per habitat (Fig. 2). Fallow lands contain the highest relative abundance of rodents and shrews with respectively 47% and 35% of captures; followed by secondary forests (35% and 31%). The lowest numbers of rodents were captured in primary forest for rodents and in wet habitats for insectivores. The comparison of different trapping techniques illustrated in Fig. 3 shows a higher capture rate for Soricidae in the pitfalls whereas rodents have a higher capture rate with Victor and Sherman traps. All species are captured regularly in all months (Table 5).

TABLE 5

TNumber of captures per species per season for the localities and during the years were these data are available (DS = dry season, WS = wet season).

Sites	year	Season	Colomys goslingi	Deomys ferrugineus	Funisciurus pyrrhopus	Funisciurus. anerythrus	Graphiurus .lorraineus	Graphiurus surdus	Hybomys lunaris	Hylomyscys stella	Hylomyscys aeta	Hylomyscys parvus	Lophuromys dudui	Lemniscomys striatus	Malacomys longipes	Mastomys natalensis	Mus minutoides	Oenomys hypoxanthus	Praomys jacksoni	Praomys mutoni	Praomys misonnei	Paraxerus boehmi	Stochomys .longicaudatus	Grammomys kuru	Total
Masako	1985	DS	2	69	0	0	0	0	60	36	8	0	13	4	8	2	4	0	101	2	19	8	16	5	369
		WS	2	87	1	0	0	2	75	72	6	3	49	28	31	0	9	1	138	9	0	6	25	19	563
	1986	DS	0	127	1	0	1	0	259	127	4	14	87	21	19	1	3	0	235	17	3	5	37	39	1000
		WS	0	105	0	0	0	1	193	98	6	16	82	22	12	0	11	0	219	3	7	4	31	13	823
Mbiye	1996	DS	1	0	0	1	2	0	0	0	0	0	8	4	9	0	0	1	63	0	0	0	0	3	92
		WS	1	0	0	1	0	0	0	0	0	0	8	1	12	0	0	0	80	0	0	0	0	5	108
	2000	DS	1	0	0	0	0	0	0	18	0	0	11	0	0	0	5	0	61	0	0	0	0	0	96
		WS	1	0	0	0	0	0	0	13	0	0	14	0	0	0	4	0	73	0	0	0	0	0	105
Yoko	1996	DS	2	0	0	0	0	0	20	7	0	0	0	5	2	0	2	0	26	0	0	0	5		71
		WS	2	0	1	0	0	0	32	5	0	0	0	0	0	0	4	2	61	0	0	0	5		112

DISCUSSION

The highest abundance was noted in fallow lands whereas the lowest is noted in primary forest and in wet habitats. This distribution probably depends on food resource availability in these different habitats. Almost all species were captured in the dry as well as in the wet season as noted by DUDU et al. (2005). The highest diversity of rodents was noted in Masako, followed by the island Kungulu and the Yoko forest reserve on the left bank. Some species such as *Suncus infinitesimus, Sylvisorex johnstoni, Sylvisorex cfr oriundus, Dendromus mystacalis* are found for the first time during our studies at Masako forest. According to COLYN & DUDU (1986), habitats with a high floral diversity usually support a high fauna diversity. Except for Masako, diversity data on shrews are still lacking. This prevents us from extending our analysis to include the Insectivora. More details on dietary analysis, feeding habit, coexistence, occurrence and food overlap of shrews in Masako forest are given in DUDU et al. (2005). STANLEY et al. (1998) reported that pitfalls are effective for surveying insectivore fauna but are less successful with larger rodents. This is confirmed by our results. The combination of snap traps, Sherman life traps and pitfalls should be more efficient to collect mid-sized small mammals.

The most abundant species in the region are *Praomys jacksoni* (34% of total captures), *Lophuromys dudui* (16%) and *Hybomys lunaris* (12%). According to DUDU and GEVAERTS (1987), *Praomys jacksoni* and *Lophuromys dudui* occur everywhere in Kisangani and its surroundings. *Lemniscomys striatus* has been collected at many sites, but occurs everywhere with a low abundance (3.56% of total captures). *Deomys ferrugineus* (7.79%) was mostly captured in Masako forest reserve and has been signalled once only at Linoko (Left bank of the Lindi river) in 1998. The absence of some species on either bank does not mean that they do not occur there because our small mammals surveys are still incomplete. For example COLYN (personal communication), found *Praomys mutoni* also on the left bank of the Congo River, although it was missing in our collections from that area. The presence of *Thryonomys swinderianus* might be recent (starting from 1992). It occurs around Kisangani as a result of forest destruction (DUDU, 1994).

Crocidura olivieri (3.70%) and *Scutisorex somereni* (0.87%) are the most abundant insectivore species occurring in all study sites and habitats. The study of Insectivora with pitfalls has only been conducted on the right bank of the Congo River and on some islands. Our study does not cover areas situated beyond 50 km of Kisangani and trapping effort was different at the different sites. This explains partly the absence of some species such as *Crocidura nigrofusca, C. goliath*, and *C. turba* collected previously in the forests between Maiko and Tshopo rivers (COLYN, 1986) in our collections. Future collections from the left bank of the Congo River should help to better understand shrew biodiversity and only part of the shrew collection data at Masako have been used in the present article.

We compared the number of terrestrial small mammals species from a number of studies carried out in different parts of the DRC (Table 6). Although the small mammal survey reported in the present paper is not exhaustive, the tropical lowland forests around Kisangani may be already be classified among the most diverse equatorial forests of central Africa as far as rodent and shrew ´species diversity is concerned.

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TABLE 6

Comparison between the number of species per genus from different studies in rainforest habitat, inside and outside the DRC. A = present study, B = Dudu, 1991, C = Colyn, 1986 (A, B, C all in the Kisangani area); D = Dieterlen & de Balzac, 1979 in the Kivu; E = Leirs et al., 1999 in Kikwit; F = ECOFAC II 2000 (Ngotto, Central African Republic; unpublished report); G = ECOFAC 2001 (Mt. Doudou, Gabon; unpublished report)

Family	Genus	A	B	C	D	E	F	G
Anomaluridae	*Anomalurus*	2	2	3		1		
Cricetidae	*Cricetomys*	1	1	1		1		
	Deomys	1	1				1	1
	Dendromys	1				3		
	Tatera					2		
Gliriidae	*Graphiurus*	2	2			1		
Muridae	*Colomys*	1	1	1		1		
	Dasymys					1		
	Gramomys			1		2		
	Heimyscus.							1
	Hybomys	1	1	1			1	1
	Hylomyscus	3	3	1		1	1	3
	Lemniscomys	1	1	1		1		
	Lophuromys	2	1	1		2	1	1
	Mastomys	1	1			1		
	Mus	1	1	1		2		
	Malacomys	1	1	1		1	1	1
	Oenomys	1	1	1		1		
	Pelomys					3		
	Praomys	3	3	2		1	1	2
	Rattus	1	1	1		1		
	Steatomys					1		
	Stochomys	1	1	1			1	1
	Thamnomys	1	1	1				1
Sciuridae	*Funisciurus*	2	2	2		2		
	Protoxerus	1		1		1		
	Paraxerus	1	1	1		1		
	Heliosciurus			1				
Hystricidae	*Atherurus*	1	1	1				
Thryonomidae	*Thryonomys*	1				1		
Potamogalidae	*Potamogale*	1	1	1				
Chrysochloridae	*Amblysomus*	1	1	1				
	Chlorotalpa					1		
Macroscelidae	*Petrodromus*	1				1		
	Rynchoyon	1	1	1				
Soricidae	*Congosorex*						1	
	Crocidura	10	9	6	9	10	12	5
	Myosorex				1			
	Paracrocidura						1	1
	Sylvisorex	2			4		3	2
	Suncus	1					1	1
	Scutisorex	1	1					
Total species		49	40	33	15	44	25	21

REFERENCES

Barbault, R. (1981). Ecologie des populations et des peuplements. Masson, Paris.

Colyn, M. (1986). Les Mammifères de forêts ombrophiles entre les rivières Tshopo et Maiko (Région du Haut-Zaïre). *Bull. Inst. r. Sci. Nat. Belg.*, 56 : 21-26.

Colyn, M. (1991). L'importance zoogéographique du bassin du fleuve Zaïre pour la spéciation : le cas des primates simiens. Paimpont,Université de Rennes, France, pp : 1-13.

Colyn, M. & A.M. Dudu (1986). Relevé systématique des Rongeurs (Muridae) des îles forestières du fleuve Zaïre entre Kisangani et Kinshasa. *Rev. Zool. Afr.*, 99 : 353-357.

Delany, M.J. (1975). The rodents of Uganda.*Trustees Brit. Mus. Nat. H.,* 8 : 165pp.

Dieterlen, V.F. & H. Heim de Balzac (1979)**.** Zur Ökologie und Taxonomie der Spitzmäuse (Soricidae) des Kivu – Gebiete. *Saügetierk. Mitt*., 27(4) : 241-287.

Dudu, A.M. (1989). Données écoéthologiques préliminaires des Rongeurs myomorphes et sciumorphes de l'île Kungulu. *Ann. Fac. Sci.* Unikis : 67-73.

Dudu, A.M (1991)**.** Etude du peuplement d'Insectivores et de Rongeurs de la forêt ombrophile de basse altitude du Zaïre (Kisangani, Zaïre). Thèse doct. inédite, Université d'Anvers : 171p.

Dudu, A.M. (1994)**.** Note de la présence de *Thryonomys swinderianus* (Temminck, 1827), le grand aulacode (Rongeurs, Thryonomidae) à Kisangani, Zaïre. *Ann. Fac. Sci.* Unikis, 10 : 159-161.

Dudu, A.M., M. Kazadi & H. Gevaerts (1985). Données préliminaires sur la distribution des Rongeurs des îles Kun-

gulu, Tundulu, et d'un biotope sur la rive gauche du fleuve Zaïre à Kisangani. *Ann. Fac. Sci*. Kisangani, 3 : 77-91.

DUDU, A. & H. GEVAERTS (1986). Notes de l'évolution des captures des rongeurs à Masako (Kisangani, Zaîre). *Ann. Fac. Sci. Kis*., sp. : 19-22.

DUDU, A.M. & H. GEVAERTS (1987). Examen de la distribution des Muridae (Rodentia, Mammalia) dans quelques associations végétales des environs de Kisangani (Zaïre). *Ann. Fac. Sci.* Unikis, 4 : 103-110.

DUDU,A., R. VERHAGEN, H. GEVAERTS & W. VERHEYEN (1997). Population structure and reproduction cycle of *Praomys jacksoni* (De Winton, 1897) and first data on the reproduction of *P.misonnei* Van Der Straeten and Dudu 1990 (Muridae) from Masako forest (Kisangani, Zaïre), *Belg. J. Zool.,* 27 (1) : 67-70.

DUDU,A., S. CHURCHFIELD & R. HUTTERER (2005). Community structure and food niche relationships of coexisting rain-forest shrews in the Masako Forest, north-eastern Congo. In : MERRITT, J.F., S. CHURCHFIELD, R. HUTTERER & B. SHEFTEL (eds), *Advances in the Biology of Shrews II* New York, Special Publ. Int. Soc. Shrew Biol., No. 1 : 229-239.

HATT, R.T. (1940). Lagomorpha and Rodentia others than Sciuridae, Anomaluridae and Idiuridae collected by the American museum Congo expedition. *Bull. Amer. Mus. Nat. Hist*., 76 : 457-604.

HOLLISTER, N. (1916). Shrews collected by the Congo Expedition of the *American Museum. Bull. Amer. Mus. Nat. Hist*.**,** 35 : 663-680.

HUTTERER, R. & D.C.D. HAPPOLD (1983). The Shrews of Nigeria (Mammalia : Soricidae). *Bonn. Zool. Monogr.* :18 : 79.

HUTTERER, R. & A.M. DUDU (1990). Redescription of *Crocidura caliginea*, a rare shrew from north eastern Zaïre (Mammalia, Soricidae). *J. Afr. Zool.*, 104 : 305-311.

KADANGE, N., T. GEMBU, G.B. KATUALA & A. DUDU, (1998). Distribution des Rongeurs et Insectivores (Mammalia) dans les habitats naturels du jardin zoologique de Kisangani (R.D. Congo). *Ann.Fac.Sci*. Unikis, 11 : 201-209.

LEIRS, H., N.J. MILLS, J.W. KREBS, J.E. CHILDS, A. DUDU, N. WOOLEN, G. LUDWIG, J.C. PETERS, T.S. KSIAZEK and other study group members (1999). Search for thee Ebola virus reservoir in Kikwit, democratic Republic of Congo. Reflection on Vertebrate collection. *The Journal of Infectious diseases*, 179, Suppl. 1 : 155-163.

LOMBA, B. & M. NDJELE (1998). Utilisation de la méthode du transect en vue de l'étude de la phytodiversité dans la réserve de la Yoko (Ubundu, RD Congo). *Ann. Fac. Sci.* Unikis, 11 : 35-46.

MEESTER, J. & H.W. SETZER (eds) (1971). *The Mammals of Africa, an Identification Manual.* Smithsonian Institution Press. Washington, D.C. pp. 1-29.

MOSANGO, M. (1991). Contribution à l'étude botanique et bio géochimique de l'écosystème forêt en région équatorial (île Kongolo Zaîre). Thèse inédite Ulb.Fac.Sci. laboratoire d'Ecologie végétale : 446p.

NICOLAS, V., P. BARRIERE & M. COLYN (2003). Impact of removal pitfall trapping on the community of shrews (Mammalia : Soricidae) in two African tropical forest sites. *Mammalia,* 67 : 133-138.

NYAKABWA, M. (1982). Phytocénose de l'écosystème urbain de kisangani, (1ère partie) Ph.D. Theses Inédit Unikis : 418p.

SCHOUTEDEN (1948) Faune du Congo Belge et du Rwanda-Urundi. Mammifères. *Ann Mus. Congo, Tervuren, Zool.,* 1 : 331pp.

STANLEY,W.T., P.M. KIHAULE, K.M. HOWELL & R. HUTTERER (1998). Small mammals of the Eastern Arc Mountains, *Tanzania. Journal of East African Natural History,* 87(1/2) : 91-100.

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A morphological assessment of *Myosorex zinki*, an endemic shrew on Mount Kilimanjaro

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ABSTRACT. The specific status of *Myosorex zinki* is analyzed based on recently collected material from Mt. Kilimanjaro. *M. zinki* historically has been viewed as a subspecies of *M. blarina*, but is distinct from *M. blarina* in several cranial dimensions. The recently collected series exhibits no sexual dimorphism. Contrary to what past records have indicated, *M. zinki* is not restricted in occurrence on the mountain and is found in many habitats on Mt. Kilimanjaro including forest, heathland, and moorland near the edge of the alpine desert. This species remains the only endemic mammalian species to Mt. Kilimanjaro.

KEY WORDS : Insectivora, Soricidae, *Myosorex zinki*, Kilimanjaro, biodiversity, systematics, Africa.

INTRODUCTION

Myosorex zinki was described as a subspecies of *Myosorex blarina* by HEIM DE BALSAC & LAMOTTE (1956) based on a skin with incomplete skull collected at 3700 m on Mt. Kilimanjaro. HEIM DE BALSAC (1967) later suggested that *M. zinki* deserved specific rank, but others retained it as a subspecies of *M. blarina* (HEIM DE BALSAC & MEESTER, 1977; HONACKI et al., 1982; SHORE & GARBETT, 1991). The need for additional specimens was often cited as required to resolve the taxonomic status of the form of *Myosorex* on Mt. Kilimanjaro. In 2002, an elevational survey of the small mammals of Mt. Kilimanjaro produced several specimens on this unique shrew, which allow us to conduct a morphological assessment of this taxon compared to *M. blarina* specimens from the Rwenzori Mountains.

MATERIAL AND METHODS

Specimens of *Myosorex* were collected during a survey of the small mammals of the south-eastern slope of Mt. Kilimanjaro conducted July and August, 2002. Five sites were surveyed at 2043, 2470, 2897, 3477 and 4000 m respectively. Both pitfall lines (for insectivores, primarily) and standard breakback traps (for rodents) were used for the collection of voucher specimens. Details on the methodology (which was identical to other small mammal surveys of montane areas of Tanzania) can be found in STANLEY et al. (1996, 1998). The *Myosorex blarina* examined in this study were all collected in the Rwenzori Mountains and are housed at the Field Museum of Natural History (Chicago, USA). The holotype of *M. blarina zinki* (SMNS 4505) was examined in the Stuttgart Natural History Museum (Germany).

Standard measurements were taken of the specimen in the field including total length, head and body length, tail length, hindfoot length, ear length and weight. All measurements were in mm except weight, which was in grams. Measurements of the cranium and mandible were made with digital calipers to the nearest 0.1 mm. These included condylo-incisive length (CI), basal length (BL), post-palatal length (PPL), length of entire upper tooth row (UTRL), length of complex teeth in upper tooth row (P4-M3), width of third upper incisor (I3W), width of canine (CW), length of third upper molar (M3L), width of third upper molar (M3W), length from first upper incisor to, and including, the upper canine (I-C), least interorbital width (LIW), bimaxillary width (BW), nasal width (NW), greatest width of the braincase (GW), height of the braincase (HBC) (measured by placing skull on microscope slide, measuring from the ventral surface of the slide to the highest point of the cranium and then subtracting the thickness of the slide from that measurement), length of mandible including the incisor (M+I), length of mandibular tooth row including first incisor (LTR), and length of the lower molars 1-3 (m1-3).

Standard descriptive statistics (mean, range, standard deviation and coefficient of variation) were derived for each taxon. We used a one-way analysis of variance to test for significant variation between sexes within *M. zinki* and between *M. zinki* and *M. blarina*. Principal components were extracted from a variance-covariance matrix using the cranial variables converted to natural logarithms. All statistical analyses were done with Excel and SPSS.

RESULTS

Summaries of external and cranial measurements for male and female *M. zinki* are presented in Table 1 and 2, respectively. There were no significant differences between sexes in either external or cranial measurements (Tables 1 and 2). All measurements were subsequently

TABLE 1

External measurements of *Myosorex zinki*. Differences between sexes were not significant (P > 0.05, see text).

External measurement	N	Total length (mm)	Head & body (mm)	Tail length (mm)	Hindfoot (mm)	Ear (mm)	Weight (g)
Male	6	129.7 ± 6.3	93.7 ± 5.4	35.8 ± 1.6	16.3 ± 1.2	7.5 ± 0.8	16.5 ± 2.3
		118-137	84-100	33-37	15-18	6-8	14.5-19.5
Female	6	130.3 ± 4.7	93.0 ± 2.4	36.2 ± 2.5	15.8 ± 0.4	7.2 ± 1.0	15.7 ± 1.2
		125-137	89-95	33-40	15-16	6-9	14-17

TABLE 2

Cranial measurements (mm) of male and female *Myosorex zinki* (mean value ± standard deviation, range) with results of a one-way ANOVA to test for sexual dimorphism.

Measurement	Males (n = 5*)	Females (n = 6)	F value	p
CI	22.9 ± 0.64 (22.1-23.7)	22.8 ± 0.61 (22.0-23.6)	0.20	0.66
BL	20.3 ± 0.63 (19.5-21.0)	20.1 ± 0.59 (19.2-20.8)	0.22	0.65
PPL	10.5 ± 0.36 (10.0-10.9)	10.4 ± 0.35 (9.7-10.7)	0.17	0.69
UTR	9.5 ± 0.20 (9.2-9.7)	9.4 ± 0.22 (9.1-9.7)	0.43	0.53
P4-M3	5.4 ± 0.18 (5.1-5.6)	5.3 ± 0.14 (5.1-5.4)	0.16	0.70
I3W	0.6 ± 0.03 (0.5-0.6)	0.5 ± 0.03 (0.5-0.6)	5.05	0.05
CW	0.7 ± 0.05 (0.6-0.7)	0.6 ± 0.02 (0.6-0.6)	2.58	0.14
M3L	1.5 ± 0.05 (1.4-1.5)	1.5 ± 0.07 (1.4-1.6)	0.05	0.83
M3W	0.9 ± 0.03 (0.8-0.9)	0.8 ± 0.05 (0.8-0.9)	0.77	0.40
I-C	4.3 ± 0.12 (4.1-4.4)	4.2 ± 0.14 (4.1-4.4)	1.48	0.25
LIW	4.9 ± 0.17 (4.6-5.0)	4.7 ± 0.10 (4.6-4.9)	2.04	0.19
BW	6.5 ± 0.17 (6.3-6.8)	6.5 ± 0.10 (6.3-6.6)	1.02	0.34
NW	2.3 ± 0.07 (2.2-2.4)	2.2 ± 0.05 (2.2-2.3)	2.93	0.12
GW	11.6 ± 0.18 (11.3-11.8)	11.5 ± 0.33 (11.1-12.0)	0.50	0.50
HBC	7.1 ± 0.11 (6.9-7.2)	7.0 ± 0.23 (6.7-7.4)	0.08	0.79
MI	14.1 ± 0.31 (13.8-14.5)	14.0 ± 0.44 (13.4-14.6)	0.33	0.58
LT	8.6 ± 0.19 (8.4-8.9)	8.5 ± 0.22 (8.3-8.8)	0.51	0.49
m1-3	4.26 ± 0.08 (4.2-4.4)	4.2 ± 0.11 (4.0-4.3)	0.34	0.57

* Sample size for HBC was 4 for males.

TABLE 3

Cranial measurements (mm) of *Myosorex blarina* and *Myosorex zinki* (mean value ± standard deviation, range) with results of a one-way ANOVA to test for significant differences between species. Measurements in bold represent those that exhibit significant differences.

Measurement	*M. blarina* (n = 4)	*M. zinki* (n = 11*)	F value	p
CI	22.0 ± 0.35 (21.5-22.3)	22.8 ± 0.59 (22.0-23.7)	6.44	0.02
BL	19.6 ± 0.36 (19.1-19.9)	20.2 ± 0.58 (19.2-21.0)	3.57	0.08
PPL	9.6 ± 0.18 (9.4-9.8)	10.4 ± 0.33 (9.7-10.9)	20.49	0.001
UTR	9.6 ± 0.24 (9.3-9.9)	9.4 ± 0.19 (9.1-9.7)	3.09	0.10
P4-M3	5.7 ± 0.19 (5.4-5.9)	5.3 ± 0.14 (5.1-5.6)	14.00	0.002
I3W	0.7 ± 0.06 (0.6-0.8)	0.6 ± 0.03 (0.5-0.6)	50.5	0.000
CW	0.9 ± 0.04 (0.9-0.9)	0.6 ± 0.04 (0.6-0.7)	165.7	0.000
M3L	1.8 ± 0.07 (1.7-1.9)	1.5 ± 0.06 (1.4-1.6)	88.9	0.000
M3W	1.1 ± 0.02 (1.0-1.1)	0.8 ± 0.04 (0.8-0.9)	118.0	0.000
I-C	4.2 ± 0.08 (4.1-4.3)	4.2 ± 0.13 (4.1-4.4)	0.001	0.97
LIW	5.4 ± 0.08 (5.2-5.4)	4.8 ± 0.14 (4.6-5.0)	53.6	0.000
BW	7.2 ± 0.13 (7.1-7.4)	6.5 ± 0.13 (6.3-6.8)	76.3	0.000
NW	2.5 ± 0.07 (2.4-2.6)	2.3 ± 0.06 (2.2-2.4)	32.0	0.000
GW	11.7 ± 0.19 (11.5-12.0)	11.5 ± 0.27 (11.1-12.0)	3.35	0.08
HBC*	7.0 ± 0.18 (6.8-7.2)	7.0 ± 0.18 (6.7-7.4)	0.07	0.79
MI	14.1 ± 0.21 (13.8-14.4)	14.1 ± 0.36 (13.4-14.6)	0.07	0.79
LT	8.8 ± 0.14 (8.6-8.9)	8.6 ± 0.19 (8.3-8.9)	4.85	0.04
m1-3	4.6 ± 0.12 (4.4-4.7)	4.2 ± 0.09 (4.0-4.4)	37.3	0.000

* Sample size for HBC for *M. zinki* was 10.

combined for a comparison of crania from *M. zinki* to samples of *M. blarina*. Coefficients of variation for cranial characters were all less than 9%. Summaries of cranial measurements for the two taxa are presented in Table 3. Out of the 18 measurements taken, 12 were significantly different (P < 0.05) between groups (one-way ANOVA;

Table 3). The initial principal components analysis indicated that four variables : I-C, GW, HBC, and MI did not contribute meaningfully to the extraction of components in multivariate space (communalities < 0.7), so these were not included in the principal components analysis. The first two components derived explained 87.5 and 5.9% of the variation, respectively. The dimensions that had the highest loadings (greater than 0.90) on the first principal component were those of breadth (LIW and BW) and width and length of teeth (I3W, CW, M3W, M3L). The second component was most heavily influenced by length variables (CI and BL), but these loadings were less than 0.90 and specimens are not clearly separated along the second component. A plot of individual specimen scores is presented in Fig. 1. The differences between the two taxa in both breadth of the skull and the dimensions of the third upper molar are exhibited in Figs 2 and 3.

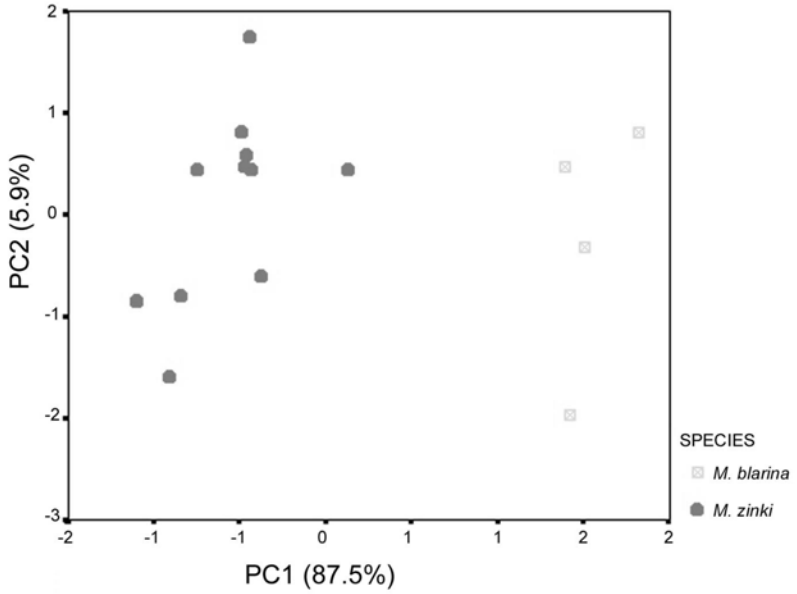

Fig. 1. – Projection of individual specimen scores on the first two principal components.

Fig. 2. – Crania of *M. zinki* and *M. blarina.*

DISCUSSION

Several authors have pointed out the distinctiveness of *M. zinki* (Heim de Balsac & Lamotte, 1956; Grimshaw et al., 1995), but the small number of specimens available until now caused some to retain the taxon as a subspecies of *M. blarina* (Heim de Balsac & Meester, 1977; Honacki et al., 1982). With the specimens now available, the recognition of *Myosorex zinki* as a species is now warranted, supporting statements by Heim de Balsac & Lamotte (1956), Heim de Balsac (1970), Hutterer (in Grimshaw et al., 1995) and others (Stanley & Hutterer, 2000).

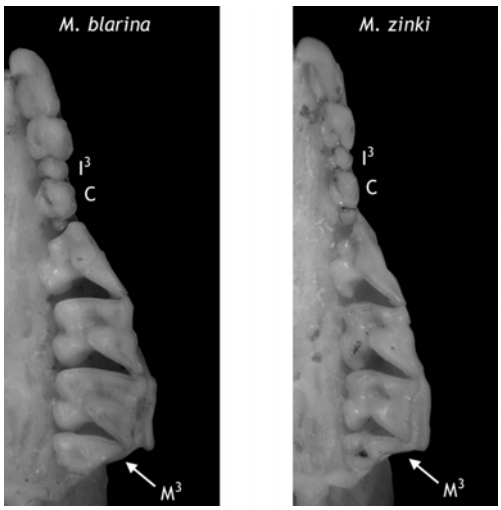

Fig. 3. – Upper tooth row of *M. zinki* and *M. blarina.*

Because of the small number of specimens previously collected and the localities of those collections, *M. zinki*

was thought to be rare and restricted in distribution on Mt. Kilimanjaro (Heim de Balsac, 1967; Grimshaw et al., 1995). A recent survey of the small mammals along the south-eastern slope of Mt. Kilimanjaro (W.T. Stanley, unpubl. data) documented the presence of this shrew in many different habitats on the mountain including forest, heathland, moorland, and the edge of the alpine desert. While it was not as abundant as other shrews at each site surveyed, *M. zinki* was the most widely distributed insectivore along the elevational gradient, ranging from 2470 to 4000 m (Fig. 4). While *M. zinki* was not documented at the lowest site (2043 m), it is too early to say it does not occur in the lower forests of Kilimanjaro.

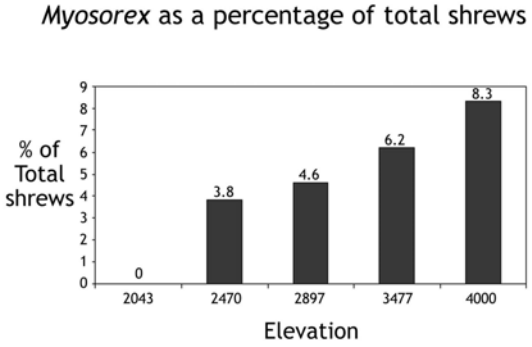

Fig. 4. – Graph of distribution of *Myosorex* along an elevational gradient on the south-eastern slope of Mt. Kilimanjaro. The numbers above each bar represent the percentage of total shrews captured at each elevation.

Myosorex zinki remains the only endemic mammal on Mt. Kilimanjaro so far, but detailed systematic study of the small mammals in eastern Africa may reveal other taxa endemic to this mountain. Burgess et al. (2000) hold that *Crocidura monax* is restricted to Mt. Kilimanjaro while other authors (Stanley et al., 2000) list this species from various Eastern Arc mountains. The problem requires careful examination. Further studies are also needed to both expand our knowledge of the ecology and distribution of *M. zinki* on Kilimanjaro and determine if it or closely related forms occur on nearby mountains, such as Mt. Meru.

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LITERATURE CITED

Burgess, N.D., D. Kock, A. Cockle, C. FitzGibbon, P. Jenkins & P. Honess (2000). Mammals. In : Burgess, N.D., & G.P. Clarke (eds), *Coastal forests of Eastern Africa*. IUCN, Gland and Cambridge : 173-190; 401-406.

Grimshaw, J.M., N.J. Cordeiro & C.A.H. Foley (1995). The mammals of Kilimanjaro. *Journal of East African Natural History,* 84 : 105-139. (appeared 1997)

Heim de Balsac, H. (1967). Faits nouveaux concernant les *Myosorex* (Soricidae) de l'Afrique orientale. *Mammalia*, 31 : 610-628.

Heim de Balsac, H. (1970). Precisions sur la morphologie et les biotopes de deux Soricidae d'altitude, endemiques du Kilimandjaro. *Mammalia*, 34 : 478-483.

Heim de Balsac, H. & M. Lamotte (1956). Evolution et phylogénie des Soricidés africains. *Mammalia*, 20 : 140-167.

Heim de Balsac, H. & J. Meester (1977). Order Insectivora. Part 1. In : Meester, J. & H.W. Setzer (eds), *The mammals of Africa : an identification manual*, Smithsonian Institution Press, Washington, D.C. : 1-29.

Honacki, J.H., K.E. Kinman & J.W. Koeppl (eds) (1982). *Mammal species of the world : A taxonomic and geographic reference*. Allen Press, Inc. and The Association of Systematics Collections, Lawrence, Kansas, 694 pp.

Shore, R.F. & S.D. Garbett (1991). Notes on the small mammals of the Shira Plateau, Mt. Kilimanjaro. *Mammalia,* 55 : 601-607.

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 Macroscelidea*). Zoologische Abhandlugen Staatliches Museum fur Tierkunde Dresden*, 49 : 131-147.

Stanley, W.T., S.M. Goodman & P.M. Kihaule (1998). Results of two surveys of rodents in the Chome Forest Reserve, South Pare Mountains, Tanzania. (Mammalia : Rodentia). *Zoologische Abhandlugen Staatliches Museum fur Tierkunde Dresden*, 50 : 145-160.

Stanley, W.T. & R. Hutterer (2000). A new species of *Myosorex* Gray, 1832 (Mammalia : Soricidae) from the Eastern Arc Mountains, Tanzania. *Bonner Zoologische Beiträge*, 49 : 19-29.

Stanley, W.T., P.M. Kihaule, K.M. Howell & R. Hutterer (2000). Small mammals of the Eastern Arc Mountains, Tanzania. *Journal of East African Natural History*, 49[for 1998] : 91-100.

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Movements, habitat use and response of ricefield rats to removal in an intensive cropping system in Vietnam

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ABSTRACT. Rapid post-control reinvasion typically hampers attempts to manage rodent pests, yet little is known about the demography or behaviours of re-invaders. Here we study the habitat use and movement of *Rattus argentiventer* using radio-telemetry during a non-breeding season (tillering growth stage of rice) and a breeding season (ripening stage of rice) in lowland irrigated rice in Vietnam. On two treatment sites, farmers removed rats by hunting, digging up burrows and by using trap barrier systems (early planted field of rice surrounded by a plastic fence set with multiple capture rat traps), and on two control sites, farmers conducted their normal control practices. The 95% minimum convex polygon home range size of rats during the non-breeding period was 2.4 ha (n = 12) and significantly smaller than during the breeding period (9.8 ha; n = 10). There was no difference in home range size between treatment (removal sites) and control sites. During the non-breeding period, rats preferred to use the bank/channel habitat during the day, and preferred vegetable habitats at night. During the breeding period, rats preferred using rice habitats both during the day and at night. This preference during the breeding period was strongly influenced by the availability of abundant cover and food offered by the mature rice crops. Rats were moving about the rice fields in random directions and were not influenced by the removal of rats at nearby locations. We conclude that even at low population densities, rodent control would need to be conducted over large areas to prevent recolonisation through random dispersal events and that rodent burrows should be destroyed during the non-breeding season when little cover is provided by crops.

KEY WORDS : habitat use, movements, ricefield rat, removal, trap barrier system, bounty system.

INTRODUCTION

Rodents are a significant problem for agriculture in Vietnam. They are considered the number one pre-harvest pests of lowland irrigated rice crops, especially in the Mekong and Red River Deltas (BROWN et al., 1999, 2003b). In particular, the ricefield rat, *Rattus argentiventer* (Robinson & Kloss, 1916), is the most common rodent found in rice crops in Vietnam, and it is an important pest of rice crops in other parts of Southeast Asia including Malaysia and Indonesia. In Indonesia, it causes annual pre-harvest losses of around 17% (GEDDES, 1992; LEUNG et al., 1999). Other rodent species inhabiting rice fields in Vietnam include *R. losea*, *R. rattus* and *Bandicota indica* (BROWN et al., 1999, 2003b). Little is known about how these rodent pest species interact with each other within the rice growing areas or how management should be implemented in a palliative manner to reduce damage to rice crops. Currently, most farmers are reactive in their control actions, only implementing management once the rat problem is moderate to severe.

Methods for controlling damage caused by rodents in rice agro ecosystems include application of rodenticides (BUCKLE, 1999), hunting, fumigation, physical barriers such as the trap barrier system (TBS, SINGLETON et al., 1998, 1999), and cultural practices such as synchronised cropping, sanitation of fields and encouraging predators (such as barn owls) (LEUNG et al., 1999). There are few data on how rat populations respond to such control actions or how quickly reinvasion occurs. Also of interest is how rats respond to control at different stages of crop development when the availability of food and cover changes, and whether there are differences in response in breeding and non-breeding seasons of the rats.

A key strategy for animals successfully reinvading areas is to have high rates of dispersal. One method for measuring rates of dispersal of small mammals into vacant areas is to experimentally remove animals from grids. SCHIECK & MILLAR (1987) studied the response of red-backed voles (*Clethrionomys gapperi*) to removal trapping in a mountain fir forest in Alberta Canada and found that about 80% of the voles caught in the removal area originated from a distance of less than two home ranges away. NAKATA & SATOH (1994) studied the response of individual grey-backed voles (*Clethrionomys rufocanus bedfordiae*) to removal trapping to determine the source of animals moving into the removal grid and the distance that these animals moved from source areas. After 2 weeks, over 90% of the voles initially located within 30 m of the edge of the removal grid were making single-direction movements towards the removal grid. Conversely, BOUTIN et al. (1985) found that only 28% of snowshoe hares (*Lepus americanus*) dispersed into removal areas and that most animals died on their home range rather than dispersing, while SULLIVAN & SULLIVAN

(1986) found that the colonization rate was 25 – 58% per four-week period.

There are few examples where researchers have monitored changes in movements of pest small mammals in natural field conditions using contemporary control methods. EFFORD et al. (2000) looked at home range changes in feral brushtailed possums (*Trichosurus vulpecula*) in New Zealand after applying an 80% control in one half of their experimental plot. They found that possums on the edge of the control area moved their home ranges towards the removal area and that the "vacuum effect" in the possums was largely confined to home range adjustments by individuals that had ranges overlapping the area of reduced density. LEIRS et al. (1997) found that recolonisation of maize fields by the multimammate rat (*Mastomys natalensis*) occurred very rapidly after a rodent control operation.

Despite the economic and social costs caused by *R. argentiventer*, its habitat use and movements in the rice agro-ecosystems of Vietnam is not well understood. In West Java, Indonesia, there are two lowland irrigated rice crops produced each year corresponding with the wet and dry seasons. *Rattus argentiventer* accounted for >95% of rodent species captured (LEUNG et al., 1999) and were found to have home ranges of 1-3 ha, with little differences between males and females, with smaller home range in the breeding season compared to the non-breeding season (BROWN et al., 2001). They mostly utilised banks (burrows) during the tillering stage of the rice crop (non-breeding period), but switch to daytime use of rice paddies throughout the ripening stage of the rice crop (breeding period) (BROWN et al., 2001). Research is therefore required in Vietnam because the cropping system and composition of rodent species are different.

As part of a large project examining the population response to a range of rodent control methods at a village-level (> 100 ha), we examined how individual rats used their environment and how they might respond to removal of other rats through the application of control techniques conducted by farmers. Specifically, we considered whether rats moved in a random pattern (classical diffusion) or directed their movement towards areas of lower population density ("vacuum effect" EFFORD et al., 2000). This was done by radio-tracking individual rats occupying rice fields on sites where farmers conducted a range of recommended rodent management practices (treated sites) and sites where farmers were not influenced in their rodent management techniques (control sites).

MATERIAL AND METHODS

Study site

The study was conducted in Vinh Phuc Province, in northern Vietnam, 40 km north of Hanoi (21°08' N; 105°45' E). Four study sites were selected to comprise part of a main village or sub-villages. Each site was 0.5 to 1 km apart and about 100 - 150 ha in size. The sites were set up in March 1999 to monitor the population dynamics of rats before implementation of ecologically based rodent management (BROWN et al., 2003b). Within each site families manage small plots of land, each 0.04 ha, and each family generally owns a total of 0.5 – 0.7 ha of land. The principal crop grown in the area is rice. There are two main rice-growing seasons each year, the spring rice season (transplanting late February and harvested mid June), and the summer rice season (transplanted mid July and harvested late September). Rice is not grown in winter because it is too cold. Other crops are vegetables (broccoli, cabbage, kohlrabi, onion, pumpkin, tomato) and flowers (chrysanthemum, rose). Summers are hot and wet, and winters are cool and dry. The annual average rainfall is approximately 1600 mm, most falling during May to September. Farmers irrigate their crops from channels using water supplied from large storage dams in nearby hills. The soil type is heavy red clays.

The radio-tracking study was conducted during the spring rice season in 2002. Rice was sown in February 2002 and then harvested in late June and early July 2002. Two sessions of radio-tracking were conducted to coincide with the non-breeding season of rats (during the tillering stage of the rice crop; March) and during the breeding season of rats (during the ripening stage of the rice crop; June).

Trapping and radio-tracking

At each site, rats were caught using single-capture wire cage traps. Traps were baited with fresh vegetables and set strategically at sites where there was obvious rodent activity to catch as many rats as possible over an area of 250 x 250 m. At each site, fifty traps were set per night for eight consecutive nights in March and six consecutive nights in June. All adult female *R. argentiventer* rats were collared on treatment and control sites and all adult male *R. argentiventer* were collared on control sites only. Resources and labour were limited so we chose not to monitor males on treatment sites. Traps were checked hourly during the first few hours after sunset and early each morning. At capture, each rat was weighed (± 2 g), sexed, and breeding condition determined and to confirm species identification and condition. Females with raised teats and perforated vagina were classified as adults, and males with descended testes were classified as adult. Prior to release, at point of capture, each rat was fitted with a single-stage radio transmitter (Sirtrack, New Zealand) attached to a nylon cable tie which functioned also as a collar around the animal's neck.

A 250 x 250 m grid of bamboo poles set 25 m apart was used to provide reference points for locating radio-collared rats. Radio tracking at all sites was conducted for up to 14 days in both March and June. Four locations or "fixes" were sought each day : one during daylight hours (0800-1400 hrs) for location of rat nests; and three after dusk (1900-2400 hrs) when rats were most active. Night fixes were 1 to 1.5 hours apart. It was not always possible to obtain three fixes for each rat after dusk. Collared rats were tracked with a hand-held 3-element Yagi antenna connected to a radio receiver. More than 80% of location fixes were tracked to within 1 m of their actual location, based on sightings of collared rats. For others, it was not possible to obtain more accurate fixes, because rats were moving around in rice paddies and would swim away before we could obtain an accurate fix. The habitat type

(large roadside bank or channel bank, rice paddy, vegetable crop, fallow, flower crop) and activity (e.g. sighted in field or known to be in a burrow) were recorded for each fix.

Home ranges were calculated from 95% and 100% minimum convex polygons (MCP) using RANGES V (KENWARD & HODDER, 1996). We calculated 95% and 100% MCP because the 100% MCP may include forays from their core areas to explore new areas and thus relevant to our hypotheses. Analyses were performed on rats that had >15 fixes, the minimum number of fixes required to estimate 80% of the home range size as found by BROWN et al. (2001) and confirmed with these data. Home ranges were ln-transformed to reduce the skewed distribution for statistical analysis. The range span was also calculated using RANGES V, and is defined as the largest distance across the MCP.

The habitat use for each rat was determined within each individual animal's home range by examining the proportion of fixes within each habitat type (OTIS & WHITE, 1999). Log ratios of usage/availability were calculated for each habitat for each rat as the basis for compositional analysis of proportional habitat use (AEBISCHER et al., 1993). Habitat availability and use was compared between months (March and June) and time of day (Day or Night). During each tracking session, the crop types grown in each field within the 250 x 250 m grid (6.25 ha) area were recorded by walking through each site. The area of channels, banks and paths was estimated by measuring their widths and lengths. The area of each habitat type was then calculated and converted to a proportion of habitat available.

Implementation of treatments

On Treatment sites (T1 and T2), two areas were set up : 1) where rats were captured and collared for radio-tracking (non-removal area, as described above), and 2) where rats were removed. Each area was 6.25 ha in size. The removal areas were 225-250 m from the non-removal areas based on average home range sizes and distances that rats would travel and get caught in a TBS (BROWN et al., 2001, 2003a). Rats were removed by the use of a tactical bounty system (SINGLETON et al., 1999), where farmers were paid 200 dong (USD$0.02 per rat) to hunt and dig rats from the removal area at a stage when rat populations abundance was low. The bounty system operated during both March and June on both Treatment sites. In addition, on T2 in June, two trap-barrier systems (TBS; SINGLETON et al., 1998, 1999) were present with sticky rice as the lure crop (variety Khang Dan, 140-150 days duration, established in late March and harvested after we concluded field work in June). On Control sites (C1 and C2), farmers conducted their normal rodent control practices.

To measure the distance and direction of movements of rats from non-removal areas the average location from the first two days of tracking (calculated by averaging X- and Y- coordinates of the first 5 -8 fixes) and the average location from the last two days of tracking (last 5-8 fixes) were calculated for each rat. Each period of tracking contained at least two daytime locations. The distances (m) and directions (bearings) moved from the first two days to the last two days were then determined. On Control sites, distances and directions towards the principal compass points (± 45° of each of N, E, S, and W) were calculated, and on Treatment sites, distances and directions towards the removal area (± 45° of N for Treatment 1, ± 45° of E for Treatment 2) and away from removal areas, were calculated.

RESULTS

In March, we trapped 51 rats from 2800 trap nights (trap success = 1.8%) in total from all sites, and in June we trapped 21 rats from 2400 trap nights (trap success 0.9%). Twenty-one adult *R. argentiventer* rats were collared for radio-tracking in March, and ten adult *R. argentiventer* rats were collared in June (Table 1). The regional abundance of rats at this time (spring) of year was generally low (mean trap success of 0.5% in March and 1.9% in June from our regular trapping locations as part of the village-level study being conducted, Fig. 1), and we believed we captured the majority of *R. argentiventer* present in the area. In March, 12 and three rats were removed by farmers by hunting and digging burrows from removal areas on Treatment 1 and Treatment 2 respectively, and in June, 63 and 50 rats were removed by farmers from removal areas on Treatment 1 and Treatment 2 respectively, most of which were juvenile animals dug from nests (evidence of active breeding on the sites).

In March, 12 rats had > 15 fixes (57% of rats captured), whereas ten rats in June had > 15 fixes (100%). Nine rats collared and released in March died from suspected poisoning (small movements, lethargic behaviour observed, or were found lying dead on the ground), one died from predation (found radio collar lying with remains of internal organs) and two were thought to be hit by farmers (fatally wounded by blow to body), whereas in June, there was no mortality of radio-collared rats during the tracking period (Table 1). If we combine deaths due to rodenticide and injury, we find that in March, farmers caused a mortality rate in collared rats of 20%, 85%, 67%, and 33% for C1, C2, T1, and T2 respectively (52% overall).

The average home range size of rats (estimated using the 95% minimum convex polygon method) in March was 2.40 ha (± 0.47 SE) and in June was 9.79 ha (± 3.31 SE) (Fig. 2). The ln-transformed home range size for female rats was significantly larger in June than in March, ($F_{1,13}$ = 4.781; P = 0.048), but there was no difference between Treated and Control sites ($F_{1,13}$ = 0.005; P = 0.947;). We could not test for differences between males and females, because no males were captured in June.

TABLE 1

Summary of radio-collared rats in March (non-breeding season) and June (breeding season) at Vinh Phuc, Vietnam. Shown are Control (C1 and C2) and Treatment (T1 and T2) sites, radio-collar frequency, sex, the number of days each animal was tracked, the number of fixes obtained, the fate of the animal, the home range sizes (ha, calculated using 95% and 100% minimum convex polygon, MCP) and home range span (m).

Tracking period	Site	Rat No.	Sex	No. days tracked	No. fixes	Fate	95% MCP	100% MCP	Span
March	C1	37	M	8	28	Alive	1.01	1.15	187
		64	M	8	28	Alive	4.99	5.07	496
		47	M	12	45	Alive	3.13	3.96	360
		241	F	7	21	Poisoned	2.32	2.33	329
		15	F	9	30	Alive	1.28	1.85	309
	C2	3	M	2	5	Poisoned	-	-	-
		6	M	2	6	Poisoned	-	-	-
		55	M	11	42	Alive	0.93	0.94	186
		60	M	6	24	Poisoned	2.10	2.27	265
		24	M	1	2	Poisoned	-	-	-
		54	M	1	2	Fatally injured	-	-	-
		41	M	2	5	Poisoned	-	-	-
	T1	75	F	9	28	Poisoned	4.18	4.59	342
		68	F	2	5	Poisoned	-	-	-
		60	F	2	3	Predation	-	-	-
	T2	25	F	12	43	Poisoned	0.14	1.33	199
		39	F	9	39	Alive	3.79	4.43	381
		43	F	2	6	Fatally injured	-	-	-
		44	F	14	52	Alive	4.19	4.83	716
		45	F	13	50	Alive	0.79	0.91	217
		49	F	1	3	Missing	-	-	-
June	C1	66	F	10	34	Alive	16.75	18.28	827
		26	F	9	30	Alive	3.83	3.85	370
		79	F	10	30	Alive	1.04	1.07	193
	C2	53	F	13	46	Alive	4.89	9.90	487
	T1	33	F	14	48	Alive	1.44	1.49	256
		73	F	13	47	Alive	2.56	2.74	287
		20	F	12	43	Alive	15.26	16.03	908
	T2	23	F	14	45	Alive	2.08	4.16	355
		71	F	13	45	Alive	17.07	19.28	755
		57	F	9	32	Alive	32.97	43.91	1433

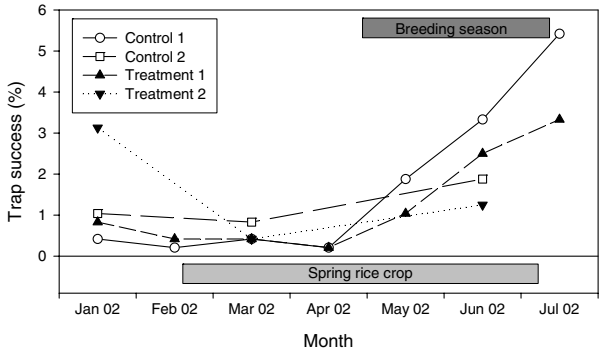

Fig. 1. – Abundance of rats (number of rats captured per 100 trap nights) on four sites used for a separate village-level study, Vinh Phuc, Vietnam from January to July 2002. Shown is approximate timing of the spring rice crop and rat breeding season (based on pregnant and lactating adult females) (P. R. Brown and N. P. Tuan unpublished data).

The home range size of rats calculated using the 100% MCP in March was 2.81 ha (± 0.48 SE) and in June was 12.07 ha (± 4.18 SE). The 100% MCP home range size in March was 0.40 ha larger on average (17.8% increase) and in June was 2.28 ha larger on average (16.3% increase) than 95% MCP. There was no significant difference in size of home ranges between the 95% and 100% MCP (paired t-test; t_{19} = -0.508, P = 0.618), therefore the 100% MCP did not provide additional information for home range analysis.

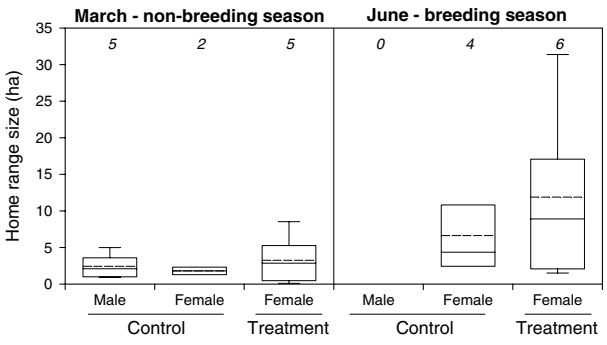

Fig. 2. – Box plot of 95% minimum convex polygon home range sizes (ha) for males and females, in treatment and control sites for March (non-breeding season) and June (breeding season). The box encloses the 25th and 75th percentiles; the solid line shows the median and the dotted line the mean home-range size. Vertical lines span the 10-90th percentiles. Sample sizes are shown at the top.

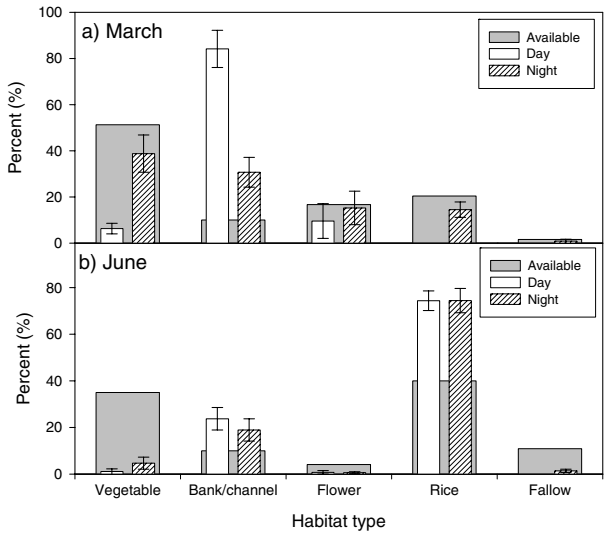

Fig. 3. – Habitat use of ricefield rats (sexes and sites combined) showing the percentage of habitats available to rats and the percentage of radio-telemetry location fixes within each habitat type for day and night fixes, Vinh Phuc Province, Vietnam 2002. (a) March, the non-breeding period for rats during the tillering stage of rice, and (b) June, the breeding period for rats during the ripening stage of rice. Error bars represent standard error of means from habitat use of individual rats.

The home range span of rats was used as an estimate of possible linear movements (Table 1). There was no significant difference between home range span between months ($F_{1,13}$ = 1.409; P = 0.256) or treatment ($F_{1,13}$ = 0.253; P = 0.624). The average home range span in March was 332.3 m (± 44.0 SE, n = 12) and in June was 587.1 m (± 123.4 SE, n = 10). This confirms that the distance between non-removal and the removal areas was set at the right distance (225-250 m).

In March, rats spent most time during the day in the bank/channel habitat (82.8% compared to 10% available) and at night most fixes occurred in the vegetable habitat (37.7% compared to 51.3% available) (Fig. 3a). Rats were not located in rice fields during the day at any stage during March. Rats used the flower habitat roughly in proportion with availability (day fixes = 10.3%; night fixes = 15.91; available 16.7%). Some rats consistently had day and night fixes in flower fields suggesting they had constructed a burrow there and were feeding within the field.

In June rats were spending more time in rice habitats with 73.2% of day fixes and 73.9% of night fixes in rice paddies compared to the 40.0% available (Fig. 3b). Rats had reduced their use of bank/channel habitats to 25.0% and 18.8% for day and night fixes respectively (compared to 10% available). Very few fixes occurred in vegetable, flower or fallow fields. The availability of crops changed between March and June because of changes in the types of crop grown.

The ratios of usage/availability confirm that in March, rats preferred to use bank habitats, and in June, rats preferred to use rice habitats and banks to a lesser extent (Table 2).

The distances moved by rats from the average of the first 2 days to the last 2 days were generally twice as large on treated sites as they were on control sites (Control March = 88.0 m ± 30.6 SE, n = 7; Treatment March = 190.9 m ± 94.0 SE, n = 5; Control June = 184.9 m ± 65.8 SE, n = 4; Treatment June = 411.8 m ± 166.1 SE, n = 6) (Fig. 4), but the distances moved were not significant (Time $F_{1,18}$ = 2.86; P = 0.108; Treatment $F_{1,18}$ = 0.278; P = 0.604; interaction $F_{1,18}$ = 0.06; P = 0.811).

The directions moved by rats on control and treatment sites were proportional with the directions available. On control sites, there were three rats that moved towards North, three to East, five to South and zero to West, with no preference for direction moved (the association between the observed directions used and directions expected was not significant : χ^2_3 = 4.636; P = 0.2004). On treatment sites, there was one rat that moved towards the removal area and 10 rats that did not move towards the removal area (1/5 rats in March and 0/6 rats in June), with no preference for direction moved (χ^2_1 = 1.778; P = 0.1824). Therefore, the direction of movements were essentially random on both control and treatment sites.

To confirm that rats were indeed breeding in June, the animals that could be retrieved were assessed for breeding condition (presence of embryos or litter of pups in the burrow). Of the three female rats recaptured, one was pregnant and two had young pups in their burrow, confirming that they were indeed breeding (100%). The breeding condition of the other females could not be ascertained because it was not possible to recapture the animals.

TABLE 2

Habitat selectivity of ricefield rats during March (tillering stage of rice crop; non-breeding season) and June (ripening stage of rice crop; breeding season) for day and night fixes for each habitat, Vinh Phuc province, Vietnam. The selectivity index is calculated by dividing the proportion of observations of rats in each habitat type by the proportion of habitat available. A selectivity value of > 1 implies preference while a value of < 1 implies avoidance.

Month	Time	Vegetable	Bank	Flower	Rice	Fallow
March	Day	0.12 ± 0.04	8.42 ± 0.81	0.57 ± 0.45	0.00 ± 0.00	0.01 ± 0.00
	Night	0.76 ± 0.16	3.07 ± 0.65	0.91 ± 0.43	0.71 ± 0.16	0.53 ± 0.52
June	Day	0.02 ± 0.02	2.37 ± 0.48	0.05 ± 0.05	3.65 ± 0.21	0.01 ± 0.00
	Night	0.09 ± 0.05	1.89 ± 0.48	0.04 ± 0.02	3.65 ± 0.26	0.86 ± 0.45

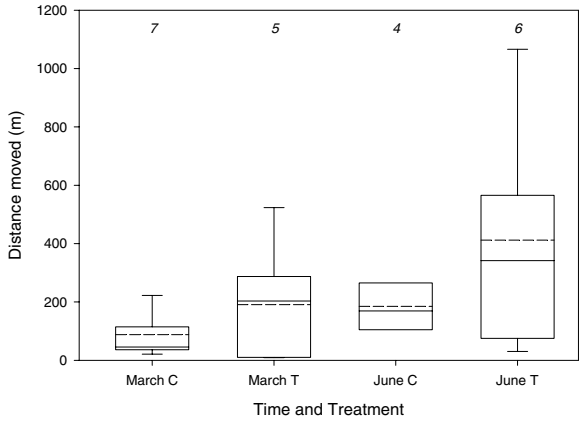

Fig. 4. – Box plot of distances (m) moved by rats from first 2 days to last 2 days of tracking on Treatment (T) and Control (C) sites in March and June 2002. The box encloses the 25th and 75th percentiles, the solid line shows the median and the dotted line the mean distance travelled, and the vertical lines span the 10-90th percentiles. Sample sizes are shown at the top.

DISCUSSION

The removal of ricefield rats during a low-density phase in an intensive cropping system in Vietnam did not induce movements of neighbouring rats towards the removal area. Rats on non-removal areas were moving randomly with regard to directions, and we believe that for *R. argentiventer*, recolonisation events during low-density phases occur through random dispersal events (classical diffusion). We could not support the "vacuum effect" proposed by EFFORD et al. (2000) for brushtail possums in New Zealand, however the density of rats in this study was low. KREBS et al. (1976) found that recolonisation rates were higher when densities of *Microtus townsendii* were higher because of competition for space, so this study should be repeated at higher densities (>10% trap success) to test this hypothesis.

It is likely that populations of ricefield rats are made up of predominantly transient animals with high rates of dispersal, as found for multimammate rats (*Mastomys natalensis*) in Tanzania (LEIRS et al., 1996). We found rats moved around a great deal, and in some cases rats had very large home ranges (> 5 ha) and did not consistently use a particular burrow or nest site. In studies conducted in both Vietnam and Indonesia, ricefield rats have recapture rates of less than 1% (BROWN et al., 1999, 2003b; LEUNG et al., 1999; JACOB et al., 2003b), and part of this reason may be because of the high proportion of transient animals. We therefore predict that rats inhabiting these highly modified and intensive rice production systems would have higher rates of dispersal than rats living in stable environments.

The home range size of rats during the non-breeding season (tillering stage, March; 2.7 ha) was of the same order as that found for ricefield rats in Indonesia (2-3 ha, BROWN et al., 2001). However, the home range size was much larger during the breeding season (ripening stage, June; 10 ha) than in Indonesia. We were surprised to find that home range sizes were larger during the breeding season. In house mice in Australia, for example, home ranges were significantly smaller during the breeding season (CHAMBERS et al., 2000). The home range size of *Rattus rattus* in macadamia nut orchards in Hawaii did not vary between males and females and did not vary through different stages of nut development (TOBIN et al., 1996). CHRISTENSEN (1996) found no seasonal variation in home range sizes of *Mastomys natalensis* in Tanzania as determined by capture-mark-release data. However, both male and female *Calomys venustus* in Argentine agroecosystems had larger home ranges during the breeding season compared to the non-breeding season (PRIOTTO et al., 2002). It is not clear why *R. argentiventer* might have a larger home range during the breeding season (June), but it could be related to the farming activities or farmers preparing for harvest. We expected that adult female rats, if they are actively breeding, would have stable, small home ranges particularly if they are caring for young in the nest. The recaptures of rats in June confirmed that the rats were indeed breeding (pregnant or suckling new born pups).

We could not prevent farmers from undertaking extraneous rodent control on our study sites. On our control sites in March, farmers poisoned nine radio-collared rats with rodenticide and two other rats died through farmers causing fatal injury. This reflects the rat control efforts employed by farmers during the tillering stage of the rice crop. Farmers are generally busy with preparations for harvest in June, so they have little time for undertaking rodent control. No deaths of radio-collared rats occurred on any site in June. The impact of these activities on this study is difficult to determine. Rats in this intensive rice growing agroecosystem are subject to a wide array of disturbances including ploughing of fields, harvesting of crops, irrigation of crops, and application of chemicals for weed or insect control. Rat populations have developed strategies for survival under these conditions through high reproductive output (LAM, 1983; TRISTIANI et al., 1998) and through their ability to recolonise areas.

Rats were using a range of habitats that were available to them, and their choice of habitat was related to cover and availability of food. When cover from tillering rice was low (March), rats were spending time in burrows in the bank/channel habitat, and when rice was ripening (June), rats were spending their time in the rice fields. We could not measure availability of food for rats, but observations made at the time showed that abundant food was always available through ripening vegetable crops such as kohlrabi, tomatoes, cabbage and broccoli, and particularly in June, abundance of maturing rice. Food was therefore probably not a limiting resource. In March, rats preferred to use the bank/channel habitat during the day, but preferred vegetable habitats at night. In June, rats preferred using rice habitats during the day and at night. This preference in June was strongly influenced by the availability of abundance cover and food offered by the maturing rice crops. These findings are similar to that found for *R. argentiventer* in Indonesia (BROWN et al., 2001).

These results suggest that there would be little point in destroying rat burrows along channels and bank habitats during the later stages of crop growth (after maximum tillering stage of rice) because rats were predominantly uti-

lising rice crops (BROWN et al., 2001). It would be interesting to monitor the changes in habitat use and movements of rats after harvest of the rice crop to see whether they revert back to using the channel/bank habitat or disperse to other habitats offering sufficient food and cover. JACOB et al. (2003a) found that the home range size of *R. argentiventer* in Indonesia decreased by 67% after harvest. The findings from the current research will help in refining appropriate management practices that farmers can use on a large scale (e.g. village level) (SINGLETON, 1997; BROWN et al., 2003b; LEIRS, 2003; JACOB et al., 2003b).

Further research is required to examine recolonisation when population densities are higher and to look at other compensatory mechanisms such as breeding performance and recruitment.

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REFERENCES

AEBISCHER, N.J., P.A. ROBERTSON & R.E. KENWARD (1993). Compositional analysis of habitat use from animal radiotracking data. *J. Wildl. Manage.,* 74 : 1313-1325.

BOUTIN, S., B.S. GILBERT, C.J. KREBS, A.R.E. SINCLAIR & J.N.M. SMITH (1985). The role of dispersal on the population dynamics of snowshoe hares. *Can. J. Zool.,* 63 : 106-115.

BROWN, P.R., N.Q. HUNG, N.M. HUNG & M. VAN WENSVEEN (1999). Population ecology and management of rodent pests in the Mekong River Delta, Vietnam. In : SINGLETON, G.R., L.A. HINDS, H. LEIRS & Z. ZHANG (eds), *Ecologically-Based Management of Rodent Pests*, Australian Centre for International Agricultural Research, Canberra : 319-337.

BROWN, P.R., L.K-P. LEUNG, SUDARMAJI & G.R. SINGLETON (2003a). Movements of the ricefield rat, *Rattus argentiventer*, near a trap-barrier system in rice crops in West Java, Indonesia. *Int. J. Pest Manage.,* 49 : 123-129.

BROWN, P.R., G.R. SINGLETON & SUDARMAJI (2001). Habitat use and movements of the rice-field rat, *Rattus argentiventer*, in West Java, Indonesia. *Mammalia,* 65 : 151-166.

BROWN, P.R., N.P. TUAN, G.R. SINGLETON, N.V. TUAT, T.Q. TAN & L.T. HOA (2003b). Impact of village-level rodent control practices on rodent populations and rice crops in Vietnam. In : SINGLETON, G.R., L.A. HINDS, C.J. KREBS & D.M. SPRATT (eds), *Rats, Mice and People : Rodent Biology and Management*, ACIAR Monograph 96, ACIAR, Canberra : 197-202.

BUCKLE, A.P. (1999). Rodenticides - their role in rodent pest management in tropical agriculture. In : SINGLETON, G.R., L.A. HINDS, H. LEIRS & Z. ZHANG (eds), *Ecologically-Based Management of Rodent Pests*, Australian Centre for International Agricultural Research, Canberra : 163-177.

CHAMBERS, L.K., G.R. SINGLETON & C.J. KREBS (2000). Movements and social organization of wild house mice (*Mus domesticus*) in the wheatlands of Northwestern Victoria, Australia. *J. Mammal.,* 81 : 59-69.

CHRISTENSEN, J.T. (1996). Home range and abundance of *Mastomys natalensis* (Smith, 1834) in habitats affected by cultivation. *Afr. J. Ecol.,* 34 : 298-311.

EFFORD, M., B. WARBURTON & N. SPENCER (2000). Home-range changes by brushtail possums in response to control. *Wildl. Res.,* 27 : 117-127.

GEDDES, A.W.M. (1992). *The Relative Importance of Pre-harvest Crop Pests in Indonesia*. Natural Resources Institute, Chatham, UK.

JACOB, J., D. NOLTE, R. HARTONO, J. SUBAGJA & SUDARMAJI (2003a). Pre- and post-harvest movements of female ricefield rats in West Javanese rice fields. In : SINGLETON, G.R., L.A. HINDS, C.J. KREBS & D.M. SPRATT (eds), *Rats, Mice and People : Rodent Biology and Management*, ACIAR Monograph 96, ACIAR, Canberra : 277-280.

JACOB, J., SUDARMAJI & G.R. SINGLETON (2003b). Ecologically-based management of rice-field rats on a village scale in West Java : experimental approach and assessment of habitat use. In : SINGLETON, G.R., L.A. HINDS, C.J. KREBS & D.M. SPRATT (eds), *Rats, Mice and People : Rodent Biology and Management*, ACIAR Monograph 96, ACIAR, Canberra : 191-196.

KENWARD, R.E. & K.H. HODDER (1996). *RANGES V - An Analysis System for Biological Location Data*. Institute of Terrestrial Ecology, Dorset.

KREBS, C.J., I. WINGATE, J. LEDUC, J.A. REDFIELD, M. TAITT & R. HILBORN (1976). *Microtus* population biology : dispersal in fluctuating populations of *M. townsendii*. *Can. J. Zool.,* 54 : 79-95.

LAM, Y.M. (1983). Reproduction in the ricefield rat *Rattus argentiventer*. *Malayan Nature Journal*, 36 : 249-282.

LEIRS, H. (2003). Management of rodents in crops : the Pied Piper and his orchestra. In : SINGLETON, G.R., L.A. HINDS, C.J. KREBS & D.M. SPRATT (eds), *Rats, Mice and People : Rodent Biology and Management*, ACIAR Monograph 96, ACIAR, Canberra : 193-190.

LEIRS, H., W. VERHEYEN & R. VERHAGEN (1996). Spatial patterns in *Mastomys natalensis* in Tanzania (Rodentia, Muridae). *Mammalia,* 60 : 545-555.

LEIRS, H., R. VERHAGEN, C.A. SABUNI, P. MWANJABE & W.N. VERHEYEN (1997). Spatial dynamics of *Mastomys natalensis* in a field-fallow mosaic in Tanzania. *Belg. J. Zool.,* 127 : 29-38.

LEUNG, L.K.P., G.R. SINGLETON, SUDARMAJI & RAHMINI (1999). Ecologically-based population management of the rice-field rat in Indonesia. In : SINGLETON, G.R., L.A. HINDS, H. LEIRS & Z. ZHANG (eds), *Ecologically-Based Management of Rodent Pests*, Australian Centre for International Agricultural Research, Canberra : 305-318.

NAKATA, K. & K. SATOH (1994). Distance of movements of voles after removal in *Clethrionomys rufocanus bedfordiae* (Rodentia : Cricetidae). *Appl. Ent. Zool.,* 29 : 97-103.

OTIS, D.L. & G.C. WHITE (1999). Autocorrelation of location estimates and the analysis of radiotracking data. *J. Wildl. Manage.,* 63 : 1039-1044.

PRIOTTO, J., A. STEINMANN & J. POLOP (2002). Factors affecting home range size and overlap in *Calomys venustus* (Muridae : Sigmodontinae) in Argentine agroecosystems. *Mammalian Biol.,* 67 : 97-104.

SCHIECK, J.O. & J.S. MILLAR (1987). Can removal areas be used to assess dispersal of red-backed voles? *Can. J. Zool.,* 65 : 2575-2578.

SINGLETON, G.R. (1997). Integrated management of rodents : A Southeast Asian and Australian perspective. *Belg. J. Zool.,* 127 : 157-169.

SINGLETON, G.R., SUDARMAJI & S. SURIAPERMANA (1998). An experimental field study to evaluate a trap-barrier system

and fumigation for controlling the rice field rat, *Rattus argentiventer*, in rice crops in West Java. *Crop Prot.,* 17 : 55-64.

Singleton, G.R., Sudarmaji, Jumanta, T.Q. Tan & N.Q. Hung (1999). Physical control of rats in developing countries. In : Singleton, G.R., L.A. Hinds, H. Leirs & Z. Zhang (eds), *Ecologically-Based Management of Rodent Pests*, Australian Centre for International Agricultural Research, Canberra : 178-198.

Sullivan, T.P. & D.S. Sullivan (1986). Resiliency of snowshoe hares to population reduction. *J. Appl. Ecol.,* 23 : 795-806.

Tobin, M.E., R.T. Sugihara, A.E. Koehler & G.R. Ueunten (1996). Seasonal activity and movements of *Rattus rattus* (Rodentia, Muridae) in a Hawaiian macadamia orchard. *Mammalia,* 60 : 3-13.

Tristiani, H., J. Priyono & O. Murakami (1998). Seasonal changes in the population density and reproduction of the ricefield rat, *Rattus argentiventer* (Rodentia : Muridae), in West Java. *Mammalia,* 62 : 227-239.

Farmer's perceptions of rodents as crop pests : Knowledge, attitudes and practices in rodent pest management in Tanzania and Ethiopia

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ABSTRACT. A study was conducted using a structured questionnaire to obtain information about the nature and extent of rodent damage to crops, farmer's perceptions of crop pests and their knowledge, attitudes and practices to their management in Tanzania and Ethiopia. The study was carried out in five localities (Makuyu -Central Tanzania; Chunya-Southwest Tanzania; Ziway and Adami Tulu (south of Addis Ababa) and Gumer/Limmo-South-west of Addis Ababa, both in Central Ethiopia). In Tanzania, maize is the major crop, both for food and sale. Other crops are sorghum, rice, simsim, groundnuts and millet. In Central Ethiopia, farmers grow maize, sorghum, teff, beans, barley, wheat, potatoes and enset. The study showed that farmers in Tanzania and Ethiopia are well aware of rodent problems and considered them to be number one pest. Rodent problems are regular and maize is the most affected crop in Tanzania. In Ethiopia, maize, enset and potatoes are the most affected crops. Maize in Ethiopia and Tanzania is susceptible to rodent damage, most seriously at planting and seedling stage. Although different rodent control techniques are practiced in Tanzania, farmers prefer using rodenticides (68.7%) to other strategies. In Ethiopia, trapping, hunting and rodenticides are the most practised techniques for rodent control. Farmer's attempts to control rodents in both countries are based on economic reasons and generally, rodent control is not undertaken when there are no crops in the fields. Farmers are responsible for rodent control activities in their individual fields. The study shows that farmers in Tanzania and Ethiopia are concerned with rodent infestation and are also aware of the critical growth stage when the crops are most susceptible. A lack of multiple rodent management methods and inadequate knowledge of appropriate and sustainable techniques appeared to be the main reasons for the over dependence on rodenticides, particularly in Tanzania. Therefore, this suggests that farmers require a strong extension input to manage rodent problems.

KEY WORDS : Rodent management, knowledge, attitudes, practices, Tanzania, Ethiopia.

INTRODUCTION

In East Africa, rodent pests are considered a major problem in agriculture and public health (MAKUNDI et al., 1999). Rodents cause considerable economic losses in staple crops, particularly tuber crops and cereals. MAKUNDI et al. (1991) reported losses of approximately 15% in cereals in Tanzania. Damage of maize at sowing and seedling stage was estimated to be 40-80% in Morogoro, Tanzania (MWANJABE & LEIRS, 1997). Widespread crop damage and losses were reported in agricultural land during rodent outbreaks in Kenya (TAYLOR, 1968). Rodent outbreaks are regularly experienced in Tanzania (HARRIS, 1937, MKONDYA, 1977; MWANJABE, 1990) and are associated with severe crop losses. According to SICHILIMA et al. (2003), considerable losses of tuber crops occur in Zambia due to infestation by mole rats. Estimates of maize damage and losses in experimental fields in Central Ethiopia indicated losses of about 26% (BEKELE et al., 2003). In Tanzania and Ethiopia, rodent control is considered the responsibility of farmers who conduct control activities individually, and rarely on a collective basis. However, in many situations, farmers have few effective technologies that can be used to reduce the impact of rodents on their crops. It has been reported, however, that the socio-economic conditions and culture of farmers influence the rodent pest management practices used (SUDARMAJI et al., 2003). Rodent pest management therefore will also be influenced by the farmer's knowledge on variables affecting crop damage, the level of crop susceptibility, the rodent pest population during the most susceptible crop stage and how much farmers are prepared to control the pests. We conducted a study in Ethiopia and Tanzania to establish farmer's perceptions and knowledge of rodents as crop pests.

MATERIALS AND METHODS

The study was carried out using a structured questionnaire developed at Sokoine University of Agriculture,

Morogoro, Tanzania. It was administered through interviews with farmers in five localities in Tanzania and Ethiopia. Two of the five localities were in Tanzania (Mvomero District and Chunya District, in Central and Southwest Tanzania, respectively). Three study locations were in Central Ethiopia (Ziway, Adami Tulu and Gummer/Limmo). Sixty farmers were interviewed in each locality. The questionnaire consisted of a series of structured questions focussing on the following :

– The size of cultivated field/family
– Ranking of the status of different pests affecting crops
– Ranking of crop damage according to crop phenology
– The proportions of fields damaged
– The rodent management techniques/approaches, and
– The most appropriate time to control rodents.

The field staff in the respective areas identified the species of rodents involved in crop damage. The data were analysed using the SPSS computer software and are presented as percentages.

RESULTS

The majority of farmers in Tanzania and Ethiopia are small landholders cultivating fields that are 1 – 2 ha in size (96.4% and 99.3% in Tanzania and Ethiopia, respectively). Most of the respondents regarded rodents as the number one pest they were least able to control. In Tanzania, 93.9% of respondents considered rodents as number one pest compared to only 3% who considered insects to be number one pest. Comparative figures for Ethiopia show that 75% of the farmers considered rodents as very important pests in their crops (Fig. 1). In both Tanzania and Ethiopia, the frequency of occurrence of rodent outbreaks was high. Regular outbreaks were reported by 66.6% and 59.7% of farmers in Chunya and Mvomero, respectively, in Tanzania. In Ziway, Adami Tulu and Gumer/Limmo, in Ethiopia, 48.7, 26.1 and 34.3% of farmers, respectively, reported regular rodent outbreaks (Table 1).

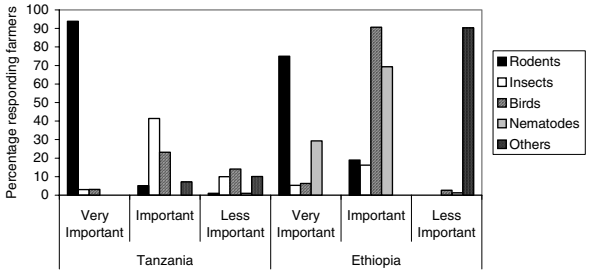

Fig. 1. – Ranking of the importance of different pests organisms in maize in farmer questionnaires in Tanzania (N = 120) and Ethiopia (N = 120)

Asked about the most susceptible crop stages, 70.4% and 82.5% of respondents in Tanzania and Ethiopia, respectively, considered seed retrieval to be most serious (Fig. 2). About 60.6% of farmers in Tanzania and 50.8% in Ethiopia indicated rodent damage to maize by seedling cutting to be serious. However, comparatively insignificant proportion of farmers in Ethiopia (1.6%) considered rodent damage to maize cobs as severe, compared to 2% of the respondents in Tanzania (Fig. 2).

TABLE 1

Frequency of occurrence of rodent outbreaks in study sites

Percentage of farmers responding					
	Tanzania		Ethiopia		
Frequency	**Chunya**	**Mvomero**	**Ziway**	**Adami Tulu**	**Gumer/ Limmo**
Regular (occurs every season)	66.6	59.7	48.7	26.1	34.3
Occasional (Occurs every few seasons)	33.3	30.3	48.7	73.9	45.7
Rare (Occurs every few years)	0	10.0	2.60	0	20.0

TABLE 2

Rodent control techniques practised by farmers in Tanzania and Ethiopia

Technique	Percent respondents practising specific rodent control technique				
	Tanzania		Ethiopia		
	Chunya	**Mvomero**	**Adami Lulu**	**Ziway**	**Gumer/Limmo**
Rodenticides	73.5	63.9	70.8	82.1	88.0
Field sanitation	4.0	2.0	12.5	2.6	17.3
Trapping	2.3	0	70.8	84.6	96.0
Hunting	2.0	0	66.7	64.1	0
Trapping and sanitation	6.1	2.0	-	-	-
Sanitation and rodenticides	17.2	0			17.2

The majority of farmers ranked maize as the most affected crop in Tanzania, with 94.9% of respondents indicating that rodent damage to maize was very important, compared to 11.0, 3.0, 4.0 and 3.0% for sorghum, millet, cassava and pulses, respectively (Fig. 3). In Ethiopia, 42.9, 90.7, 4.5 and 98.7% of the respondents reported rodent damage as very important in pulses, enset, barley and potatoes, respectively, but not in teff (Fig. 3).

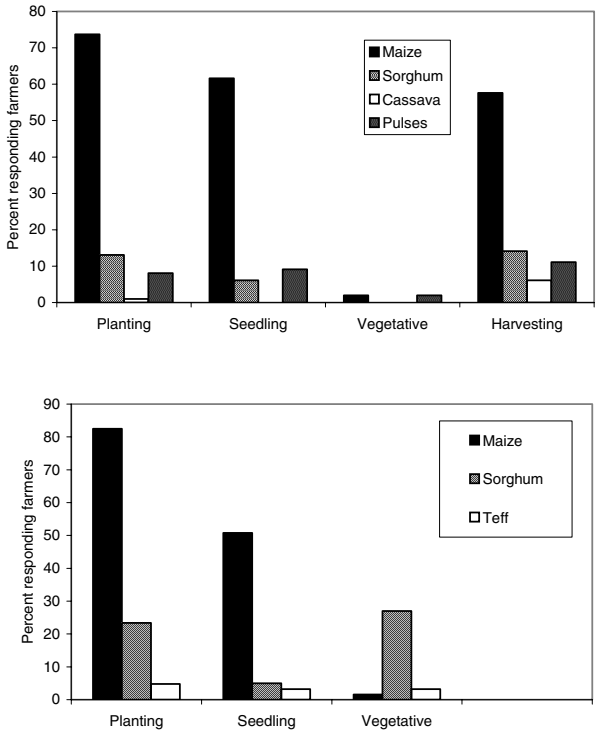

Fig. 2. – Rank
ing of rodent damage to crops at different crop growth stages in farmer questionnaires in Tanzania (top, N = 120) and in Ziway and Adami Lulu, Ethiopia (bottom, N = 120)

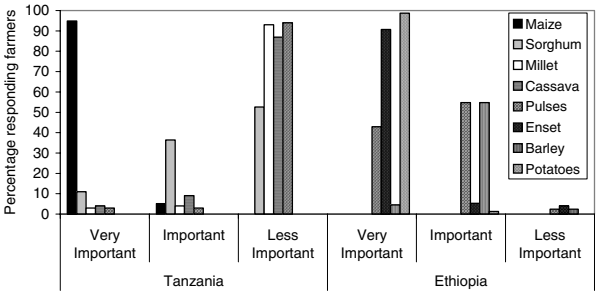

Fig. 3. – Ranking of the importance of rodent damage to specific crops in farmer questionnaires in Tanzania (N = 120) and Ethiopia (N = 180)

In Tanzania, the majority of farmers indicated using rodenticides (73.5 and 63.9% of respondents for Chunya and Mvomero, respectively) to control rodents, with much lower proportions of respondents using field sanitation/ and or field sanitation and rodenticides (17.1% of respondents for Chunya and none for Mvomero), hunting and other strategies (Table 2). Although more respondents (70.8, 82.1 and 88.0% for Adami Tulu, Ziway and Gummer/Limmo, respectively) in Ethiopia were using rodenticides, the other control approaches were also more widely practised than in Tanzania (Table 2). For maize, farmers applied control measures more often before planting (Table 3). In Ethiopia more farmers continued to apply control measures after planting maize (Table 3a) than was the case in Tanzania (Table 3b).

TABLE 3A

Time most appropriate for rodent control in Ethiopia

Village	Percentage of farmers controlling rodents	
	Before planting	After planting
Adami Tulu	91.7	8.3
Ziway	97.4	2.6
Gumer/Limm	96.3	3.7

TABLE 3B

Time most appropriate for rodent control in Tanzania

Village	Percent of farmers controlling rodents	
	Before planting	After planting
Chunya	98.3	1.7
Mvomero	97.6	2.4

DISCUSSION

The damage to crops by rodents and the subsequent yield losses at harvest is economically significant since farmers in both countries are small landholders with little alternative incomes, other than from their staple and cash crops. Farmers ranked rodents as number one pest, probably because they are least able to control them compared to the other pests. In similar studies conducted in South East Asia, SUDARMAJI et al. (2003) in Indonesia and TUAN et al. (2003) in Vietnam reported that farmers perceived rodents as the most important pests in their crops. The regular occurrence of rodent outbreaks reported by the majority (64.6%) of respondents in Tanzania is consistent with earlier reports (HARRIS, 1937; CHAPMAN et al., 1959; MKONDYA, 1977; MWANJABE, 1990; unpublished reports Rodent Control Center, Morogoro, Tanzania, 1990-1998). Occurrences of rodent outbreaks in East Africa were also recorded by TAYLOR (1968) and KEY (1990). The farmer's knowledge on manifestations of rodent damage to cereals is also consistent with previous field observations reported by MAKUNDI et al. (1999); MWANJABE & LEIRS (1997) and recently by MULUNGU et al. (2003). MWANJABE & LEIRS (1997) reported maize damage of 40-80% in the seedling stage in Tanzania, while 20% damage was reported in Kenya (TAYLOR, 1968). In experimental fields in Ziway, Ethiopia, where the study was conducted, rodent damage to maize seedlings averaged 12.6% leading to 26.4% yield loss (BEKELE et al., 2003). In the current study, 82.5% of farmers in Ethiopia experienced seed retrieval by rodents, while 50.8% reported damage to seedlings. However, BEKELE et al. (2003) reported that an important part of the damage to maize occurred after the seedling stage. It is therefore possible that seed retrieval by rodents has no serious consequences on final yields

compared to seedling cutting since farmers replant to replace missing seedlings. As the rain season progresses, it becomes impossible to replace cut seedlings and therefore, any further seedling cut by rodents affects the potential yield of the crop (MULUNGU, 2003). Most farmers applied control measures before rather than after planting, which reduces the rodent infestation in the fields. From a management point of view, this is the most appropriate time particularly for a maize crop because the necessity to replant, which is costly in terms of labour and the cost of replacing the seeds, will no longer be there.

Farmers practise a range of techniques to control rodents in both countries but control is based on economic reasons. The reliance on rodenticides appears to be related to effectiveness of this technique, particularly when rodent population densities are high (MAKUNDI et al., 1999). However, the costs involved may be prohibitive for farmers to use this technique. In Tanzania, however, government intervention in the form of free supplies of rodenticides, distribution and supervision of bait application is done only during outbreaks of rodents but not for routine rodent control. A comparison of the rodent control measures shows that there is more integration of approaches in Ethiopia than in Tanzania, partially attributed to lack of free supplies of rodenticides in Ethiopia. Farmers also apply control measures more intensively before planting than after planting. In the study localities in Tanzania, a good proportion of the farmers also continued to apply rodent control measures after planting indicating that rodents were considered a threat to the maize crop in the early stages of growth. This indicates farmer's awareness and knowledge on when reduction of damage by rodent control is most effective and is consistent with earlier reports that more severe damage of the crop occurs at planting and seedling stage (MAKUNDI et al., 1999). In the study sites in Tanzania and Ethiopia, different rodent species were responsible for the reported damage to crops. In both countries farmers have local names to differentiate between species. In Central Tanzania, *Mastomys natalensis* was the dominant and most abundant pest species, where as in Southwest Tanzania, two species, namely *M. natalensis* and *Tatera leucogaster* were responsible for the reported damage. In Central Ethiopia, BEKELE et al. (2003) reported that *Arvicanthis dembeensis* and *M. erythroleucus* were the major pest species whereas *Mus mohamet* and *Tatera robusta* were minor pest species. In Tanzania, 46.5% of farmers considered maize cob damage to be serious, compared to only 1.6% in Ethiopia. This is possibly due to differences in the species found in the study localities. In Tanzania, *M. natalensis* is a good climber and has been reported to damage cobs on standing maize stems (MULUNGU, 2003). Similar findings have not been reported for the species found in Ethiopia.

CONCLUSIONS

The study shows that farmers in Tanzania and Ethiopia experience severe crop damage due to rodents and that rodent control is undertaken for economic reasons. Rodents are considered the number one pest species in both countries. Further, farmers are aware of the most vulnerable stages when severe attack of crops occurs. Measures taken to control rodents are much more integrated in Ethiopia than in Tanzania, but generally they rely on rodenticides to a greater extent than on the other control measures. The study also shows that *M. natalensis* and *Tatera leucogatser* are the major pest species in the study localities in Tanzania, whereas *Arvicanthis dembeensis* and *M. erythroleucus* are the major pests in Ethiopia.

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REFERENCES

BEKELE, A., H. LEIRS & R. VERHAGEN (2003). Composition of rodents and damage estimates on maize farms at Ziway, Ethiopia. In : SINGLETON, G.R., L.A. HINDS, C.J. KREBS and D.M. SPRATT (eds). *Rats, Mice and People* : *Rodent Biology and Management*. ACIAR Monograph 96 : 262-263.

CHAPMAN, B.M., R.F. CHAPMAN & D. ROBERTSON (1959). The growth and breeding of the multimammate rat, *Rattus natalensis* (Smith) in Tanganyika Territory. *Proceedings of Zoological Society, London*, 133 : 1-9.

HARRIS, W.V. (1937).The grey field mouse. *The East Aafrican Agricultural Journal*, 2 : 315-318.

KEY, G.E. (1990). Pre-harvest crop losses to the African stripped ground squirrel, *Xerus erythropus*, in Kenya. *Tropical Pest Management*, 36 : 223-229.

MAKUNDI, R.H., N.O. OGUGE & P.S. MWANJABE (1999). Rodent Pest Management in East Africa – An Ecological Approach. In : SINGLETON, G., L. HINDS, H. LEIRS & Z. ZHANG (eds). *Ecologically-based Rodent Management*. Australian Center For International Agricultural Research, Canberra, Australia : 460-476.

MAKUNDI, R.H., T.J. MBISE & B.S. KILONZO (1991). Observations on the role of rodents in crop losses in Tanzania and control strategies. *Beitrage zur Tropischen Landwirtschaft und Veterinarmedizin (Journal of Tropical Agriculture and Veterinary Science),* 29(4) : 465-474.

MKONDYA, C.B. (1977). Preliminary proposals and hints for approaches to outbreak evaluation and control strategies against rodent infestation in the Shinyanga outbreak foci in Tanzania. Dar es Salaam, Ministry of Agriculture, Crop Development Division.

MULUNGU, L.S. (2003). Assessment of maize (*Zea mays* L.) damage and yield loss due to rodents in the field. *PhD Thesis*, Sokoine University of Agriculture, Morogoro, Tanzania. 178p.

MULUNGU, L.S., R.H. MAKUNDI & H. LEIRS (2003). Robustness of techniques for estimating rat damage and yield loss in maize fields. In : SINGLETON, G.R., L.A. HINDS, C.J. KREBS & D.M. SPRATT (eds). *Rats, Mice and People* : *Rodent Biology and Management*. ACIAR Monograph 96 : 224-228.

MWANJABE, P.S. & H. LEIRS (1997). An early warning system for IPM based rodent control in small holder farming systems in Tanzania. *Belgian Journal of Zoology*, 127 : 49-58.

MWANJABE, P.S. (1990). Outbreaks of *Mastomys natalensis* in Tanzania. *African Small Mammal Newsletter*, 11 : 1.

Sichilima, A.M., M.S. Zulu & H. Leirs (2003).The effects of *Tephrosia vogelii* and land preparation methods on mole rat activity in cassava fields. In : Singleton, G.R., L.A. Hinds, C.J. Krebs & D.M. Spratt (eds). *Rats, Mice and People* : *Rodent Biology and Management*. ACIAR Monograph 96 : 254-255.

Sudarmaji, G.R. Singleton, N.A. Herawati, A. Djatihari & Rahmini (2003). Farmer's perceptions and practices in rat management in West Java, Indonesia. In : Singleton, G.R., L.A. Hinds, C.J. Krebs & D.M. Spratt (eds). *Rats, Mice and People* : *Rodent Biology and Management*. ACIAR Monograph 96 : 389-394.

Taylor, K.D. (1968). An outbreak of rats in agricultural areas of Kenya in 1962. *East African Agricultural and Forestry Journal*, 34 : 68-71.

Tuan, N.P., Ss.J. Williams, P.R. Brown, G.R. Singleton, T.Q. Tan, D.T. Hue, P.T.T. Ha & P.T. Hoa (2003). Farmer's perceptions and practices in rat management in Vinh Phuc Province, northern Vietnam. In : Singleton, G.R., L.A. Hinds, C.J. Krebs & D.M. Spratt (eds). *Rats, Mice and People* : *Rodent Biology and Management*. ACIAR Monograph 96 : 399-402.

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Rodent population fluctuations in three ecologically heterogeneous locations in northeast, central and south-west Tanzania

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ABSTRACT. Rodent population fluctuations and breeding patterns were investigated at localities in South-west, Central and North-east Tanzania. The three localities are ecologically heterogeneous in vegetation types, rodent species diversity, rainfall pattern and altitude. Capture-Mark-Release studies were conducted in 2001-2003 to compare rodent species composition and population trends. In North-eastern Tanzania, species composition is diverse and includes *Mastomys natalensis*, *Lophuromys flavopunctatus*, *Grammomys dolichurus*, *Arvicanthis nairobae*, *Praomys delectorum* and *Mus* sp.. Five species were recorded in South-western Tanzania namely, *M. natalensis*, *Graphiurus murinus*, *Saccostomus elegans*, *Tatera leucogaster* and *Steatomys pratensis*. In Central Tanzania *M. natalensis* was dominant, but a few *Lemniscomys griselda* were captured. Rodent abundance fluctuations were distinctively seasonal, especially for *M. natalensis* in the three localities and *T. leucogaster* in South-west Tanzania. In North-eastern Tanzania, *L. flavopunctatus*, *G. dolichurus*, *A. nairobae and P. delectorum* had low, but relatively stable populations throughout the year. In South-west Tanzania, population peaks of *M. natalensis* and *T. leucogaster* were reached in the dry season (June-September). In Central Tanzania, breeding of *M. natalensis* was seasonal, with highest population abundance during July-November. Female *M. natalensis* were reproductively active in January-May and males had scrotal testes in December-June. No males were sexually active during July-November. Female *T. leucogaster* in South-western Tanzania were reproductively active during November-April/May whereas sexually active males appeared in the population during November-March. In view of the observed rodent population fluctuations and breeding patterns, recommendations are given for pragmatic rodent control in South-west and Central Tanzania and for plague in North-eastern Tanzania.

KEY WORDS : *Mastomys natalensis*, *Tatera leucogaster*, *Grammomys dolichurus*, *Lophuromys flavopunctatus* sp., *Praomys delectorum*, *Saccostomus elegans*, *Graphiurus*, *Mus*, *Arvicanthis nairobae*, Tanzania, population fluctuation, crop damage, plague.

INTRODUCTION

In Tanzania, rodent populations exhibit a range of densities within and between seasons and years. Temporal variations in rodent density have been reported for various species, including the most common pest, *Mastomys natalensis*. TELFORD (1989), LEIRS (1992) and CHRISTENSEN (1996) reported densities of 1125, 900 and 384 animals/ha, respectively, in Morogoro, Tanzania. For a species whose breeding characteristics are strongly dependent on rainfall patterns, such fluctuations are expected to be the rule rather than the exception (MAKUNDI & MASSAWE, 2003). Population fluctuations of *M. natalensis* are influenced by density dependent and density independent factors occurring simultaneously, which regulate population size (LEIRS et al., 1997). Although much emphasis has been directed towards understanding the effect of weather on rodent population dynamics in Tanzania (TELFORD, 1989; LEIRS, 1992; MWANJABE & LEIRS, 1997; etc), the intrinsic characteristics of the species and nature of habitats have received much less attention. For example, it is more common for certain species populations to fluctuate more widely in certain types of habitats than in others, but the mechanisms underlying such fluctuations are little known. For this reason, ecologically heterogeneous areas may be expected to exert different influences on resident rodent species leading to varying levels of population fluctuations. Changes in population density of rodents, particularly the occurrence of high numbers at the most susceptible stage of crop growth, may have severe consequences on crop damage and losses. In plague outbreak foci, these changes could also influence the severity of disease outbreak and dissemination. We therefore investigated population fluctuations of different species of rodents in three ecologically heterogeneous localities in Tanzania in view of providing a pragmatic approach for effecting control measures to reduce rodent damage to maize crop at sowing and seedling stage and for plague control.

MATERIALS AND METHODS

Study sites

The study was conducted in northeast, central and southwest Tanzania. In Northeast Tanzania (NET), the study was carried out at two locations, Manolo and Magamba, in Shume Ward, Lushoto District, in the western Usambara Mountains. Shume ward is located north of

Lushoto town (04º 42' 16"S, 38º 12'16'E). The area has a single, but asymmetrical rainy season, extending from October to May. November/December and March/April are the wettest months (Fig. 2). The dry season is from July to September. There were two permanent trapping sites in the western Usambara Mountains. At the Magamba locality, a grid was set adjacent to the montane rain forest in an area reserved for agro-forestry at an altitude of 1730 m above sea level (a.s.l.). The grid was located on a steep slope and was planted with trees including *Gravillea robusta* and evergreen bushes. The Manolo study area was at an altitude of 1826 m a.s.l. The grid was set in permanent fallow land and bushes, surrounded by fields of maize, fruit trees and *Gravillea robusta*. Much of the grid had bushes whose vegetation was dominated by *Rumex usambarensis*. The Manolo and Magamba study sites are about 15 km apart.

In Chunya District, South-west Tanzania (SWT), the climate is characterized by a long dry season from April to November (Fig. 5). There is a single rainy season from December to March, but the amount of rainfall varies considerably between years. Chunya District has a hilly landscape, with vegetation characterised by miombo woodlands, scattered acacia trees and bush thickets. However, the study area was in the flat low lands in the Lake Rukwa basin within the Rukwa Rift Valley. It is characterised by miombo woodlands opened for agriculture, although the soils are of low fertility. Wooded savannah grasslands of *Acacia commiphora* bushlands and *Brachystegia julbernadia* woodlands dominate the uncultivated areas. Crops in cultivated fields included sorghum, sunflower, maize and cassava. The farms are generally small in size and fallow patches between fields are common, which increases the heterogeneity of the habitats. Overgrazing, particularly in the long dry season, leaves most of the landscape virtually bare of vegetation. The study sites consisted of two grids, located in Chang'ombe village (08º 46'S 33º 18'E), at an altitude of 600 m a.s.l. The two grids, coded CHB and CHC, were about 4 km apart and are within the Lake Rukwa basin. Grid CHB was under maize cultivation for several years before the study, but was maintained fallow throughout the study period. Grid CHC was communal land that had been maintained fallow, with many acacia trees and bushes before and during the study. In the dry season, it was subjected to grazing by cattle and goats. The grids were dominated by grass species, particularly the guinea fowl grass, *Rotthboelia cochinchinensis* and the bobbin weed, *Leucas martinnicensis.*

In Central Tanzania (CTZ), the study was conducted at two sites in Mvomero District. Each of the localities (Makuyu and Milama) (06º 22'S 37º 38'E) had two grids (MKA and MKB for Makuyu; MLA and MLB for Milama). The two localities were about 5 km apart and grids were approximately 300-400 m apart. The grids in Makuyu were fields under maize cultivation before the study but were maintained fallow throughout the study period. Fields under maize cultivation surrounded the grids. The grids in Milama were located in a large land block (>25 ha) owned by a local Catholic Mission. The land, which had not previously been under crop cultivation, was fallow and had several tree species dominated by kapok, but was also occasionally used for grazing cattle and goats by the neighbouring villagers. The study site in Makuyu (MKA and MKB) had several species of grasses, dominated by *Pennisetum* spp., *R. cochinchinensis* and *Cymbopogon* spp. These study sites were more uniform in vegetation type, and therefore were less heterogeneous. The rain patterns shows two rainy seasons; the short rainy season is from November to end of December, sometimes extending to January (Fig. 3b). In some years, no rains, or very little rains are received in this season. The long rains season (March-May) is characterized by heavy downpour except in some years when it is marginal.

Although the three study sites in NET, CTZ and SWT are ecologically heterogeneous, there is a strong human impact on vegetation and climate. The study sites in NET were part of the tropical moist forest covering most of the Usambara Mountains. However, a large proportion of the natural montane forest has been cleared for agriculture and pine plantations. The extended wet season, supplemented by irrigation, allows intensive cultivation of various crops including cereals, beans, various vegetables, and fruits. Temperatures are on average 18-22^{0}C and frost is regularly experienced on the ground when the temperature falls below 10^{0}C at night, particularly in July and August.

In CTZ, the area is extensively cultivated, but bushes and fallow patches of land intersperse between individual small fields, creating a vegetation mosaic. Flourishing opportunistic weeds in and around crop fields are common during the rainy season, but these are ploughed into the soil or burned during land preparation in the following season. When the short rains are adequate, the fields are cultivated with maize and sorghum, but the main cropping season is during the long rains. In SWT, cultivated fields and grasslands for grazing dominate the landscape, but large patches of woodland are scattered in the Lake Rukwa Valley.

Rodent trapping

Two 100 x 100 m grids were set in each locality, except in CTZ where there were a total of four grids (coded MKA, MKB, MLA and MLB). In each grid there were one hundred trapping stations at 10 m apart, with a single Sherman trap set per station. Trapping of rodents was conducted for three consecutive nights every month from May 2002 and April 2003 in NET, January 2001 to April 2003 in SWT and January 2001 to May 2003 in CTZ. Captured animals were identified, marked by toe clipping, weighed and the breeding conditions were recorded. In males, the breeding condition was determined by the position of the testes, whether scrotal or abdominal. In females, the breeding condition was determined either by signs of pregnancy by palpation, lactation, and/or perforate vagina. Animals were released at the point of capture soon after the data were recorded. Population density estimates were determined in the programme CAPTURE.

RESULTS

Table 1 shows the principal habitat type and species richness in the three study localities. Species richness was higher in the forest/agro-forestry habitats in NET and the savannah grassland, woodland and cultivated fields in SWT, than in the extensively cultivated fields in CTZ.

TABLE 1

Location of study sites, principal habitat type and rodent species richness.

Species captured	Western Usambara Mountains (NET)	South west Tanzania (SWT)	Central Tanzania (CTZ)
	Forest and agro-forestry habitats	Savanna grasslands, woodlands and cultivated fields	Cultivated fields, crop-fallow mosaics
Mastomys natalensis	X	X	X
Mus sp.	X		
Grammomys dolichurus	X		
Arvicanthis nairobae	X		
Lophuromys flavopunctatus	X		
Praomys delectorum	X		
Graphiurus sp.		X	
Tatera leucogaster		X	
Saccostomus elegans		X	
Steatomys sp.		X	

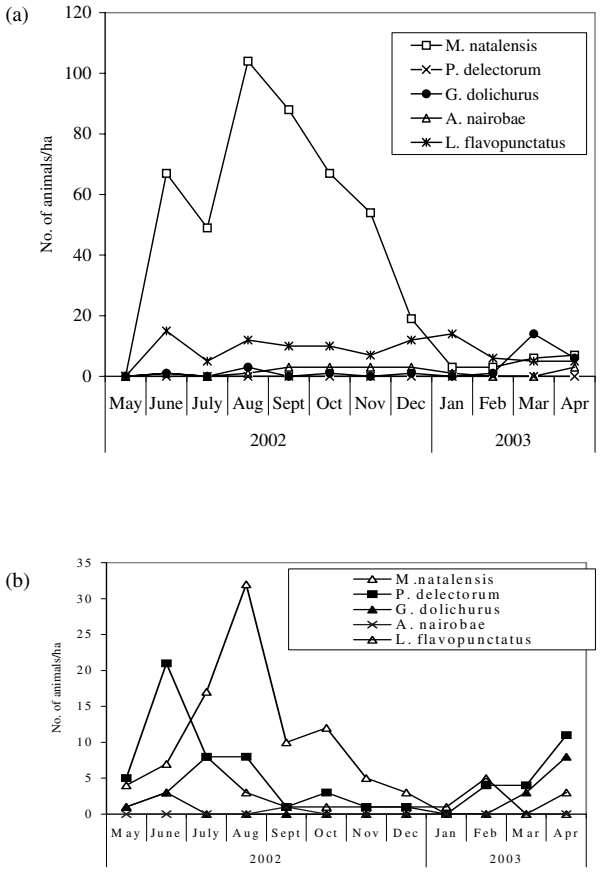

Fig. 1. – Rodent population density fluctuations at Manolo (a) and Magamba (b) in the Western Usambara Mountains, northeast Tanzania.

Fig. 1 shows the rodent population trends for different species in NET. In both study sites, the population density of *M. natalensis* was higher than for the other rodent species. Populations of *M. natalensis* reached 100 animals/ha and 33 animals/ha in Manolo (Fig. 1a) and Magamba (Fig. 1b) study sites, respectively, in August. The lowest population density was in January, with less than 5 animals/ha in both sites. *Praomys delectorum*, *Grammomys dolichurus*, *Arvicanthis nairobae* and *Lophuromys flavopunctatus* showed less marked fluctuations with less than 10 animals/ha. In NET, *A. nairobae*, a savannah species, was relatively abundant in February-May compared to other months. It is also obvious that more *P. delectorum* were captured in Magamba, where the grid was adjacent to the natural forest than in the Manolo site. *L. flavopunctatus* was found more abundantly in the secondary bush/forest fallow land inter-phase. Fig. 2 shows the rainfall pattern in the western Usambara Mountains. July-September were the driest months. Populations of *M. natalensis* peaked in August during the dry season and gradually declined towards January. Breeding individuals of *M. natalensis* occurred in the population in higher proportions during March-August and March-June for males and females, respectively (Figs 3a and 3b).

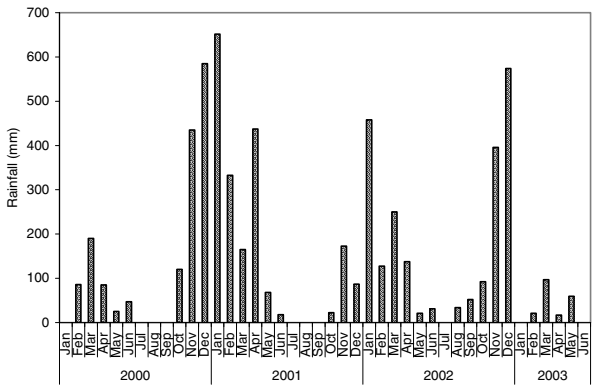

Fig. 2. – Rainfall pattern in Lushoto, Western Usambara Mountains, northeast Tanzania.

Fig. 4 shows the rodent population fluctuations in the Rukwa Valley (SWT). High populations of *M. natalensis* occurred, particularly between July and September, when densities were close to 200 animals/ha. The population density of *Tatera leucogaster* in SWT remained below 40 animals/ha throughout the year. The abundance and population densities of *Graphiurus murinus, Saccostomus elegans* and *Steatomys* sp. were relatively low. Fig. 5 shows the rainfall pattern in SWT, with a long dry season from May to October. Figs 6a and 6b show the population trends of female and male *M. natalensis* and the proportions of individuals in breeding condition. Sexual activity in females extended from February to May, with peak

activity in March/April. Breeding activity was associated with the onset of the rains and population peaks were reached in the dry season. For males, reproductively active individuals appeared in the population in January until end of April. *T. leucogaster* also showed a seasonal activity in breeding, which was concentrated in the wet season (November-April). Females with perforated vagina, in lactating or in pregnant condition were found in the population from November to April (Fig. 7). Reproductive activity for males followed a similar pattern, with sexually active individuals appearing in the population from November to March (Fig. 8).

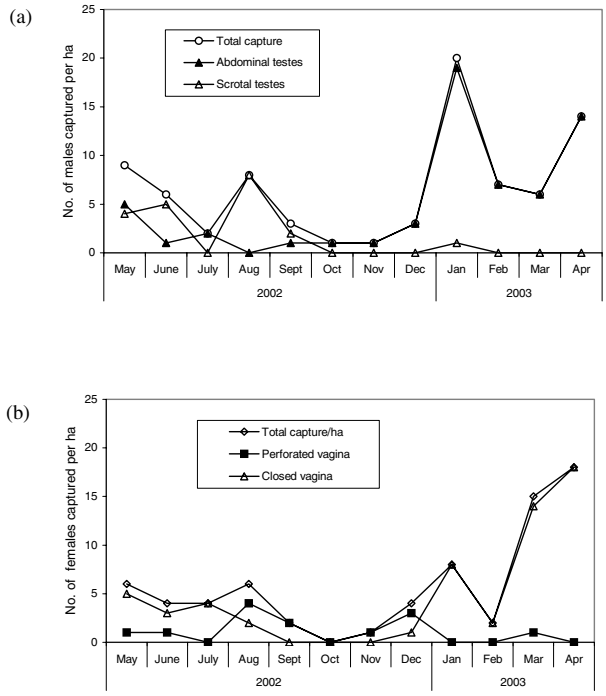

Fig. 3. – Reproductive conditions of male (a) and female (b) *Mastomys natalensis* at Manolo, Western Usambara Mountains, northeast Tanzania.

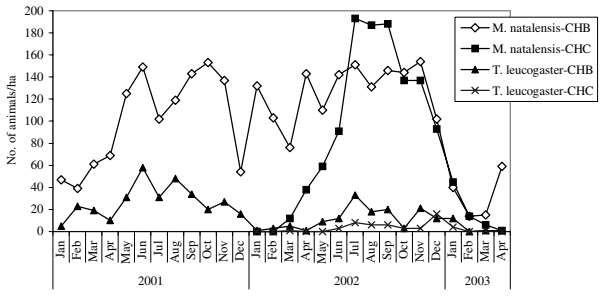

Fig. 4. – Rodent population density fluctuations in Chunya, Lake Rukwa Valley, southwest Tanzania.

Fig. 9 shows rodent population density fluctuations in CTZ. In this locality, only *M. natalensis* were captured in large numbers, and showed dramatic fluctuations with highest peaks of population density in July- November. This coincided with the beginning of the dry season and the onset of the short rain season (Fig. 10). Breeding activity reached peak between September and February for females (Fig. 11a) and December-March for males (Fig. 11b).

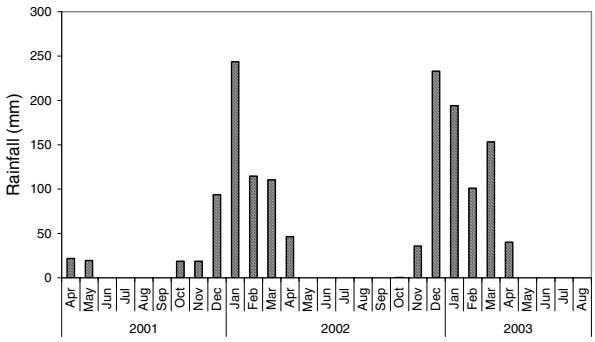

Fig. 5. – Rainfall pattern in Chunya, Lake Rukwa Valley, southwest Tanzania.

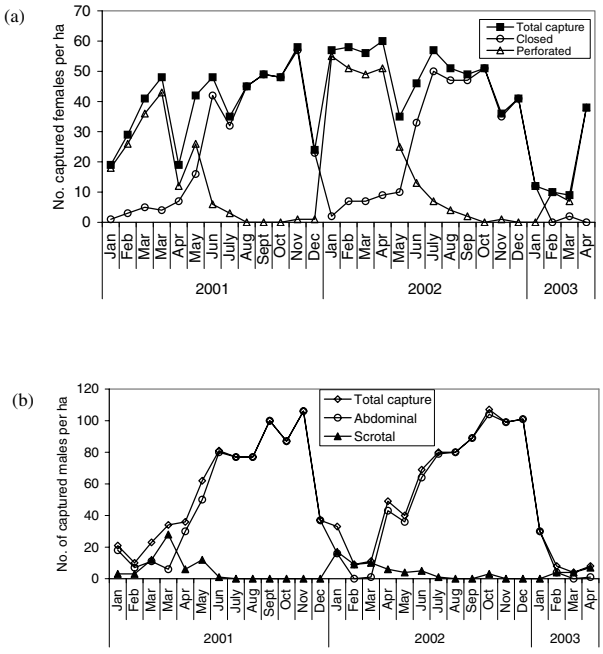

Fig. 6. – Breeding condition of female (a) and male (b) *Mastomys natalensis* in Chunya, Lake Rukwa Valley, southwest Tanzania.

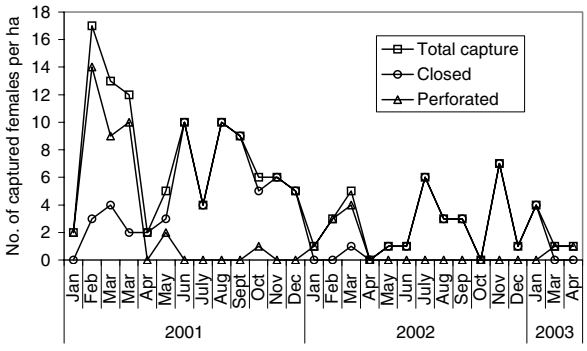

Fig. 7. – Breeding condition in female *Tatera leucogaster* in Chunya, Lake Rukwa Valley, southwest Tanzania.

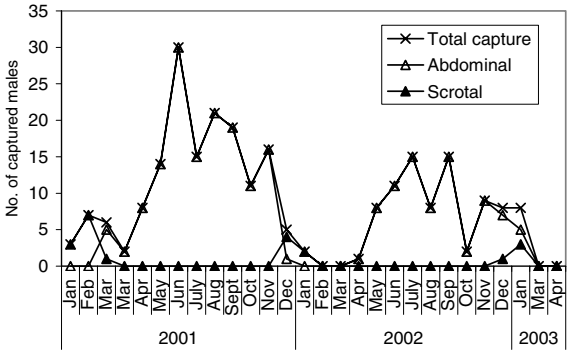

Fig. 8. – Breeding condition in male *Tatera leucogaster* in Chunya, Lake Rukwa Valley, south-west Tanzania.

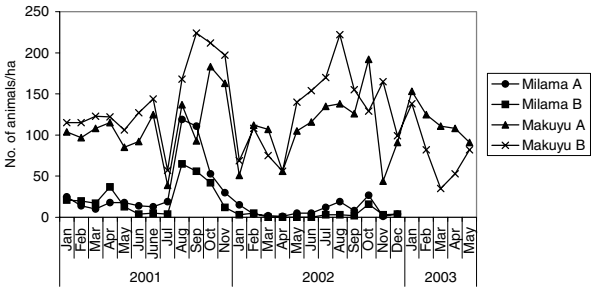

Fig. 9. – Rodent population density fluctuations in Mvomero, Morogoro, central Tanzania.

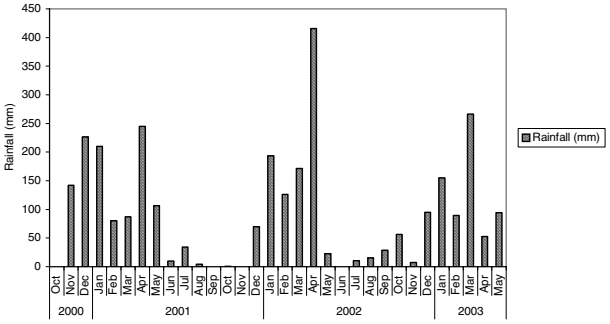

Fig. 10. – Rainfall pattern in Mvomero, Morogoro, central Tanzania.

DISCUSSION

Populations of *M. natalensis* underwent drastic increases and declines in numbers, particularly in SWT and CTZ. In SWT, *M. natalensis* and *T. leucogaster* were relatively abundant, but *T. leucogaster* maintained a consistently low population density. The fluctuations of the population of *M. natalensis* in CTZ followed a trend reported by LEIRS (1992). Tropical rodent species populations are generally influenced by many factors, but rainfall is considered as a principal factor determining the onset of breeding activity and reproduction (DELANY, 1986; LEIRS, 1992 and references therein). Temporal eruptions and extinctions of populations of *M. natalensis* were observed in the three localities in primarily fallow and agricultural land. It is apparent that land subjected to agriculture is a more variable habitat for *M. natalensis* and populations may fluctuate greatly as resources change in quality and quantity. The ecological changes that have occurred (including vegetation and climate) as a result of human activity, including opening of the woodlands and wooded grasslands in SWT and clearing of the natural forest in NET for agricultural development, have affected the spatial distribution and temporal fluctuations in density of rodent species. In NET, colonization by savannah species of rodents, mainly *M. natalensis* and *A. nairobae*, is probably due to habitat changes brought about by agriculture (MAKUNDI et al., 1999). In all the three localities, a much more detailed study is required to elucidate the species specific habitat requirements, which not only determines the species distribution, but also temporal fluctuations.

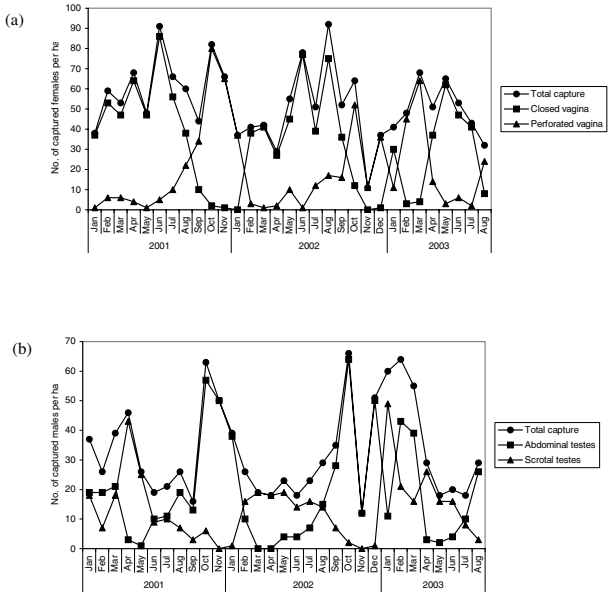

Fig. 11. – Breeding conditions of female (a) and male (b) *Mastomys natalensis* in Mvomero, Morogoro, central Tanzania.

The relationship between rainfall, breeding activity and fluctuations in numbers is obvious in the three localities. Breeding occurred during and after the rains in all the localities. The population peaks were reached in the dry season. The influence of rainfall on breeding of *M. natalensis* has been widely reported (e.g. LEIRS, 1992; DELANY, 1974; TELFORD, 1989). In the three study sites, food resources probably influenced to a great extent the fluctuations in rodent population density, but with greater influence in SWT and CTZ than in NET. It is also noticeable that there were some local effects on breeding of rodents, probably mediated through food resources in the three localities. Similar observations were made by SWANEPOEL (1978) who reported that in an agricultural area, *P. natalensis* were breeding during winter in irrigated wheat fields, but not in the natural vegetation. It has also been suggested that abundant high quality food in the absence of predation can induce population fluctuations to outbreaks proportions (HUBERT & ADAM, 1985), probably due to among the factors, the effects on breeding. In most Muridae in Africa breeding occurs during the most favourable time when resources are most abundant (DELANY, 1972; CHEESEMAN & DELANY, 1979). The abundance and quality of these resources most certainly

increases survival and recruitment of young leading to increases in population density.

The study sites in SWT and NET supported more species of rodents than in CTZ. Apart from the variations in rainfall patterns in the three localities, differences in habitat types were very pronounced. Habitat heterogeneity in terms of vegetation structure was more pronounced in SWT and NET than in CTZ, where extensive cultivation was practised. The wooded savannah grasslands of *Acacia commiphora* bushlands and *Brachystegia julbernadia* woodlands and cultivated fields with fallow patches in the uncultivated areas were prominent habitats in SWT. This probably accounted for the higher species richness than in CTZ. In NET the agro-forest fields adjacent to the natural moist forest and the forest itself, were the dominant habitats for rodent species. These two habitats were more complex in vegetation structure and microhabitats, and therefore could also explain the higher number of species recorded.

It is known that environmental factors can influence populations of the same species at different locations (KREBS, 1999). The more heterogeneous habitat complexes in NET supported fewer individuals and had much lower fluctuations of population density. The forest dwelling species in NET showed less dramatic density fluctuations indicating occupation of a much more predictable and stable habitat. In general, species that inhabit relatively stable habitats show less dramatic changes in numbers compared to those inhabiting unstable habitats (ODUM, 1966). These species have probably reached a stable equilibrium in which fluctuations only occur within limits set by the available resources, which do not show marked seasonal variations. *M. natalensis* appeared to respond to increased food resources in the aftermath of the rains by fast breeding and greater recruitment of young than the other species in SWT and NET. *Mastomys natalensis* was found predominantly in the cultivated land and in fallow land, which are much more unstable habitats compared to forest and woodlands. In NET, the intensive cultivation throughout the year, sometimes with low or little ground cover and few fallow patches between individual fields is probably not favourable for a large build-up of rodent populations, including *M. natalensis*.

In SWT, *T. leucogaster* generally maintained a consistently low population with no major fluctuations in density. This species occupied the same habitat as *M. natalensis* and experienced similar environmental conditions and yet the fluctuations were low. This could probably be attributed to competition for seeds and other resources with the numerically dominant *M. natalensis*. The same speculation could have accounted for the low numbers of *A. nairobae* in NET where *M. natalensis* was relatively dominant numerically.

Implications on rodent control

In SWT and CTZ, rodents are associated with severe crop losses, particularly maize at sowing and seedling stages. At the onset of the long rains in CTZ and SWT, rodent populations are still high for maize crop damage to occur at sowing and seedling stage. Therefore, it is important to control rodents in both CTZ and SWT to prevent maize crop damage. The observed population density fluctuation patterns suggest that rodent management will be more effective in reducing seed depredation and seedling damage if carried out before and during planting and early during the seedling stage of the maize crop. TELFORD (1989) suggested that rodent control should be concentrated between January and the onset of the long rains in CTZ, a duration of 2-3 months. However, this is not practical for poor resource farmers, with only about 0.5-1.0 ha of maize fields. Since maize is most susceptible to rodent damage in the first 2 weeks after planting (MAKUNDI et al., 1999), a single treatment with bromadiolone or zinc phosphide, as currently practised in Tanzania may not be effective enough as fields are soon invaded by rodents 1-2 weeks after saturation baiting. A more pragmatic approach arising from observations from this study, and a general recommendation for all parts of Tanzania experiencing similar problems, will be to carry out saturation baiting with either broamadiolone or zinc phosphide or other recommended rodenticide three times; the first a week before planting, the second during planting and the third at the beginning of the second week after planting. This recommendation assumes that most or all farmers shall carry out control activities simultaneously.

In NET, human plague outbreaks occur in October-March when populations of rodents are low (Fig. 1a). This can be attributed to presence of "free" fleas, seeking for alternative hosts at low rodent densities (MAKUNDI & MASSAWE, 2003; MAKUNDI et al., 2003). A different approach for plague control in this locality is recommended. To avoid increasing mortality pressure on already declining populations of rodents and also not to increase the population of 'free' fleas without a host in the environment, the most practical approach will be to intensify control of fleas with insecticides and applying rodent control only in houses where *Rattus rattus* is dominant. This kind of approach is different from current practices in which rodent control is intensified during plague outbreaks within and outside houses.

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REFERENCES

CHEESEMAN, C.L. & M.J. DELANY (1979). The population dynamics of small rodents in a tropical Africa grassland. *Journal of Zoology London*, 188 : 451-475.

CHRISTENSEN, J.T. (1996). Home range and abundance of *Mastomys natalensis* (Smith, 1834) in habitats affected by cultivation. *African Journal of Ecology*, 34 : 298-311.

DELANY, M.J. (1986). Ecology of small rodents in Africa. *Mammal Review*, 16(1) : 1-41.

DELANY, M.J. (1974). *The ecology of small mammals*. Edward Arnold, London.

DELANY, M.J. (1972). The ecology of small rodents in tropical Africa. *Mammal Review*, 2 : 1-42.

HUBERT, B. & F. ADAM (1985). Outbreaks of *Mastomys erythroleucus* and *Taterillus gracilis* in the Sahelo-Sudanian zone in Senegal. *Acta Zoology Fennica*, 173 : 113-117.

KREBS, C.J. (1999). *Ecological Methodology.* Addison Wesley Longman, Menlo Park, California.

LEIRS, H. (1992). *Population ecology of Mastomys natalensis (Smith 1834) : Implication for rodent control in Africa.* PhD Thesis, University of Antwerp, Antwerpen, Belgium.

LEIRS, H., N. STENSETH, J.D. NICHOLS, J.E. HINES, R. VERHAGEN & W. VERHEYEN (1997). Stochastic seasonality and non-linear dependent factors regulate population size in an African rodent. *Nature*, 389 : 176-180.

MAKUNDI, R.H, N.O. OGUGE & P.S. MWANJABE (1999). Rodent Pest Management in East Africa – An Ecological Approach. In : SINGLETON, G., L. HINDS, H. LEIRS, H. & Z. ZHANG (eds). *Ecologically-based Rodent Management*. Australian Center For International Agricultural Research, Canberra, Australia : 460- 476.

MAKUNDI, R.H. & A.W. MASSAWE (2003). Review of recent advances in studies of the ecology of *Mastomys natalensis* (Smith 1834) Rodentia (Muridae) in Tanzania, eastern Africa. In : SINGLETON, G.R.; L.A. HINDS, C.J. KREBS & D.M. SPRATT (eds). *Rats, mice and people : Rodent biology and management.* ACIAR Monograph 96 : 242-245.

MAKUNDI, R.H., B.S. KILONZO & A.W. MASSAWE (2003). Interaction between rodent species in agro-forestry habitats in the western Usambara mountains, northeast Tanzania, and its potential for plague transmission to humans. In : SINGLETON, G.R.; L.A. HINDS, C.J. KREBS & D.M. SPRATT (eds). *Rats, mice and people : Rodent biology and management.* ACIAR Monograph 96 : 20-24.

MWANJABE, P.S. & H. LEIRS (1997). An early warning system for IPM-Based rodent control in smallholder farming systems in Tanzania. *Belgian Journal of Zoology*, 127 : 49-58.

ODUM, E.P. (1966). *Ecology.* HOLT, RINEHART and WINSTON, New York-Chicago-San Francisco-Toronto-London : 152p.

S, E.P. (1966). *Ecology.* Holt, Rinehart and Winston, New York-Chicago-San Francisco-Toronto-London : 152 p.

SWANEPOEL, C.M. (1978). *Demographic changes associated with a Praomys natalensis population which is transient between wheat field and grassland habitats.* M.Sc. Thesis, University of Rhodesia, Salisbury.

TELFORD, S.R. JR. (1989). Population biology of the multimammate rat, *Praomys* (*Mastomys) natalensis* at Morogoro, Tanzania 1981 – 1985. *Bulletin Florida State Museum Biological Series*, 34(6) : 249-287.

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Social organization of the Eastern Rock Elephant-shrew (*Elephantulus myurus*) : the evidence for mate guarding

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ABSTRACT. Understanding the costs and benefits of defending solitary females, or mate guarding, may be the key to understanding the evolution of monogamy in most mammals. Elephant-shrews, or sengis, are a unique clade of small mammals that are particularly attractive for studies of mate guarding. We studied the spatial organization of Eastern Rock Sengis (*Elephantulus myurus*) in KwaZulu-Natal, South Africa, from August – December 2000. Our objectives were to describe the home ranges of males and females using radiotelemetry, noting the sizes and overlap of adjacent ranges and how the spatial organization changes through time. Males and females were spatially associated in monogamous pairs despite the fact that males contributed no obvious direct care to offspring. These monogamous associations persisted despite the fact that some males had home ranges large enough to encompass multiple females. Males also had more variable ranges, perhaps because they spent more time at the periphery of their ranges exploring for the presence of additional females. There was likely competition for females, as range shifts were observed when male territory holders died or disappeared. It seems likely that this species is a model study organism to investigate the costs and benefits of mate guarding.

KEY WORDS : Social organization; *Elephantulus myurus*; mate guarding, monogamy.

INTRODUCTION

Elephant-shrews or sengis (KINGDON, 1997) are a unique group of small mammals with no ecological or behavioral equivalents outside of Africa. All species feed largely on invertebrates (RATHBUN, 1979; CHURCHFIELD, 1987; KERLEY, 1995), and all are highly cursorial and capable of very fast locomotion (RATHBUN, 1979). The smaller species usually produce only one or two offspring that are born in a very precocial state. These life histories are more similar to small-bodied cursorial herbivores than similar-sized small mammals. Behaviorally, all of the 15 species of sengis from 4 genera are suspected to be monogamous (RATHBUN, 1979). Of the species studied in detail, male and female pairs have overlapping territories that result in monogamous associations, probably for life (SAUER, 1973; RATHBUN, 1979; FITZGIBBON, 1995, 1997). Territory defense is same-sex specific, and despite their nearly congruent territories, males and females spend little time together except during estrus, when the male continuously attends and follows the female (RATHBUN, 1979). Scent-marking appears to be an important component of pair bond maintenance (LUMPKIN & KOONTZ, 1986; KOONTZ et al., 1999). Males are also known to occasionally visit neighboring territories, typically resulting in intrasexual aggressive interactions (RATHBUN, 1979).

Recent molecular work indicates that sengis are a part of an early radiation of African mammals that is represented by the extant golden moles, tenrecs, the aardvark, hyraxes, sea cows, and elephants (HEDGES, 2001; MURPHY et al., 2001). Consensus is building to place all of these mammals in the Superorder Afrotheria (MURPHY et al., 2001). All studies have indicated that elephant-shrews represent a monophyletic group (CORBET & HANKS, 1968; TOLLIVER et al., 1989), and there exists no other group of closely related mammals that are all suspected to be monogamous.

Monogamy is one of the more evolved forms of social organization in mammals and is found in fewer than 10% of mammalian species (KLEIMAN, 1977; KLEIMAN & MALCOLM, 1981). Monogamy in mammals has traditionally been proposed to be due to either the necessity for male care (obligate monogamy) or due to female dispersion (facultative monogamy; KLEIMAN, 1977, 1981; WITTENBERGER & TILSON, 1980; SLOBODCHIKOFF, 1984; BARLOW, 1988). There is no evidence to suggest sengi males engage in any direct paternal care activities, especially since the young are so precocial.

The objectives of this study were to describe the spatial organization of the Eastern Rock Sengi (*Elephantulus myurus*, Thomas and Schwann 1906) to determine if this species exhibits monogamous association patterns in natural populations. *Elephantulus myurus* is distributed in southern Zimbabwe, western Mozambique, eastern Botswana, and eastern South Africa on rocky outcrops in semi-arid savannahs (NEAL, 1995). Unlike other elephant-shrews, *E. myurus* do not travel along a network of trails; rather they use their swift cursorial gait to travel from rock to rock (RIBBLE, personal observation). The primary breeding season of *E. myurus* in southern Africa is August-March, with minimal breeding from April-July (STOCH, 1954; WOODALL & SKINNER, 1989; NEAL, 1995). Females are typically anestrus from May to July (VAN DER HORST & GILLMAN, 1941). We described the social organization of *E. myurus* by determining the home

ranges of males and females, noting the size and overlap of adjacent ranges and if the spatial organization changes through time. Since no studies on the social organization of this species had been previously conducted, we were also interested in noting any features of the social organization that would provide insight into the evolution of monogamy in elephant-shrews.

METHODS

We studied the social organization of *E. myurus* on a 10-ha rock outcrop at Weenen Nature Reserve, located in the KwaZulu-Natal province of South Africa (S28°52.5398' E030°00.2193'), from August through December 2000. Weenen is a 4183-ha game reserve with habitats characterized by open, acacia savannahs with tall grasses (e.g. *Hyparrhenia* spp. and *Themeda triandra)* and thicker woodlands (e.g. *Acacia karoo*) along valley bottoms and riparian corridors (PERRIN & TAOLO, 1999a, 1999b).

Individuals were trapped on the outcrop with Elliot aluminum traps baited with peanut butter and oats, and occasionally supplemented with chopped-up insect parts (DU TOIT & FOURIE, 1992). Captured elephant-shrews were recorded, ear-tagged, and a streak of hair dye was applied to either their back or sides for visual recognition. In the early morning, *E. myurus* were readily observed basking on rocks, which made it easy to confirm that we had marked all individuals in the population.

To document home ranges of individuals, we attached "mouse-style" radiotransmitters (SM-1, AVM Instrument Company, Ltd., Colfax, CA) around the necks of sengis with plastic cable-ties. This was accomplished by physically restraining the animals, avoiding the use of anesthesia. Radiotransmitters weighed on average 3.20 $\pm$ 0.07 (1SE) g, which was 5.3 $\pm$ 0.15 % of their average weight of 60.5 $\pm$ 1.1 g. Individuals were radiotracked with an AVM receiver attached to a 3-element Yagi antenna. Many of the radiolocations were confirmed with visual sightings (33%). During the night individuals were visible with a strong headlamp and seemed unconcerned with our presence. Some locations were determined by removing the antenna coaxial cable from the receiving antenna and waving the lead over the boulder where the elephant-shrew was taking refuge. Individuals were recorded as "active" if they were moving about or "resting" if they were stationary. The Universal Transverse Mercator (UTM) coordinates of locations were ascertained with a Garmin GPS 12 receiver (Garmin International, Inc.). The receiver was left in place at the radiolocation for 10 min to calculate the average position determined from satellites during the entire 10-min interval. We conducted experiments that indicated this 10 min point-averaging feature resulted in a reading that was within 1.8 $\pm$ 0.3 (1*SE*) m of subsequent readings at the same spot (RIBBLE, unpublished data).

After trapping the rock outcrop and conducting preliminary radio-tracking on 5 individuals in August, we attempted to radiotrack all adult individuals located in the outcrop the next 3 months. Since individuals were marked with hair dye and visible in the morning hours basking on rocks and no individuals were observed outside the rock outcrop, we were confident that we were tracking all adults. Individuals were radiotracked for 4 – 8 days (mean = 6 $\pm$ 1.8 days) during each session each month. At the start of the study, radiotransmitters were removed after each session. It became apparent that these elephant-shrews handled the radiotransmitters with no apparent problems. Pregnant females gained their expected weight and successfully weaned offspring while radiocollared. Towards the end of the study radiotransmitters were left on individuals for as long as 50 days. On average, individuals actually gained 0.14 ± 0.09 g per day while carrying radiotransmitters (range –0.03 to 0.83 g per day). Radiotracking observations were taken at all hours of the night and day because preliminary observations indicated *E. myurus* could be active at any time. Individual locations were separated by at least one hour to avoid autocorrelation of data (SWIHART & SLADE, 1985).

We collected home-range data on each radiotagged *E. myurus* during 2 to 4 (mean = 2.7) monthly sessions during this study. Animals were trapped at the beginning of each radiotelemetry session to check their reproductive status and replace radiotransmitters that quit working. The last radiotracking session was conducted in November, and animals were trapped in December in order to remove their radiotransmitters. The minimum convex polygon (MCP) of all radiolocations and trap locations during a monthly session was recorded as the home range for each individual for that month. We accepted statistical significance at $P \leq 0.05$.

RESULTS

From 10 to 14 adult *E. myurus* were observed on the study outcrop each month (Table 1). The number of males and females was most often equal except in September when the sex ratio was 7males :4 females. Females were first observed lactating in September, and the first juveniles were observed and trapped in October.

Radiotelemetry indicated that individuals were active at any hour (Fig. 1), although activity was reduced in the middle of the night (ca. 2300 – 0500h) and the middle of the afternoon (ca. 1200 – 1700h). Individuals were most active and furthest from their home range centre between 1800 and 2300h. During the morning activity period (ca. 0600 – 1100h), *E. myurus* spent most of their time basking on the tops of boulders, presumably warming their body temperature (MZILIKAZI et al., 2002).

The mean monthly home-range size for males (3958 $\pm$ 625 m^2) was larger than females (2011 $\pm$ 130 m^2; $P \leq 0.05$). Across all monthly radiotelemetry sessions, seven males had home ranges that were at least twice the size (range 8204 – 13487 m^2) of the mean monthly female home range of 2011 m^2. The average number of intrasexual overlaps each month was 0.9 and 0.4 for males and females, respectively, which was not significantly different. Intrasexual overlap was greater for males than females (18 vs. 2%; $P \leq 0.05$). The home-range data from November 2000 are representative of the monthly patterns (Fig. 2), showing the lack of overlap between adjacent females. Female ranges tended to be overlapped by only one male, but there were cases where one female range was overlapped by more than one male (see female 777 overlapped by males 724 and 738; Fig. 2).

TABLE 1

Summary of spatial and temporal relationships of *Elephantulus myurus* at Weenen Game Reserve, South Africa, 2000. Horizontal bars represent life span and location of individuals. A dotted line indicates individual was alive, but not paired. Adult individuals (boldface numbers) within same boxes were presumably paired and their offspring (italic numbers) are included in the same box. (arrow = Home-range shift; d = disappearance; X = mortality; *O* = offspring)

Individuals	Gender	August	Sept	Oct	Nov	Dec
719	♀	d				
718	♂					
766	♀					
783	♀				*O* d	
784	♀				*O*	
720	♀				d	
724	♂					
775	♂			*O*	d	
776	♂			*O*		
806	♀					
777	♀					
738	♂				X	
805	♂					
770	♀			d		
773	♂		d			
721	♂					
774	♀					
771	♀					
723	♂			d		
772	♀		*O* d			
736	♂				X	
810	♂					

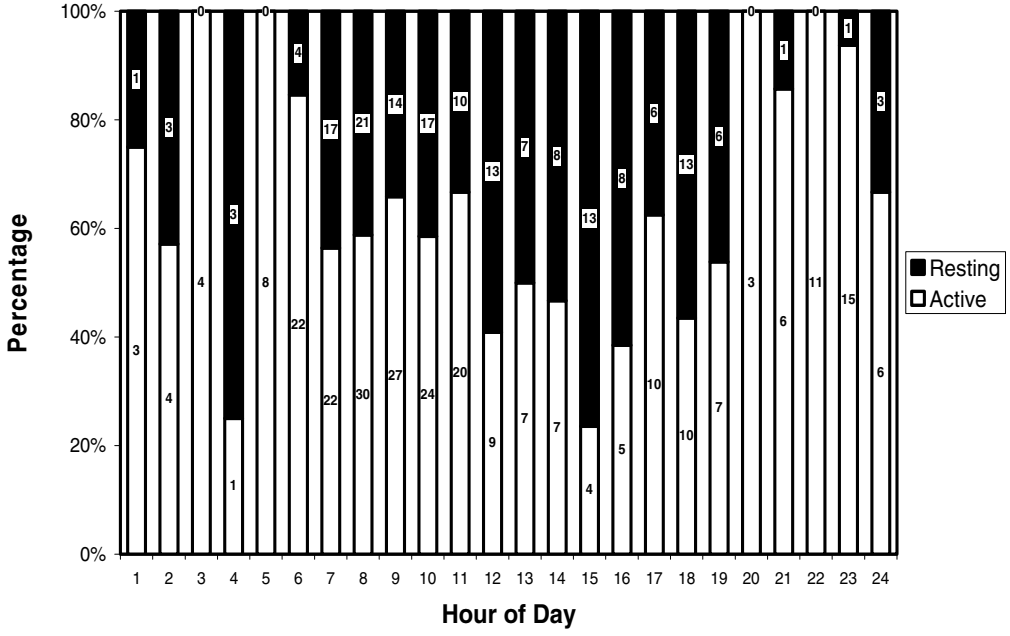

Fig. 1. – Activity patterns of radio-collared *Elephantulus myurus* during the entire study. Sample sizes are indicated for each bar.

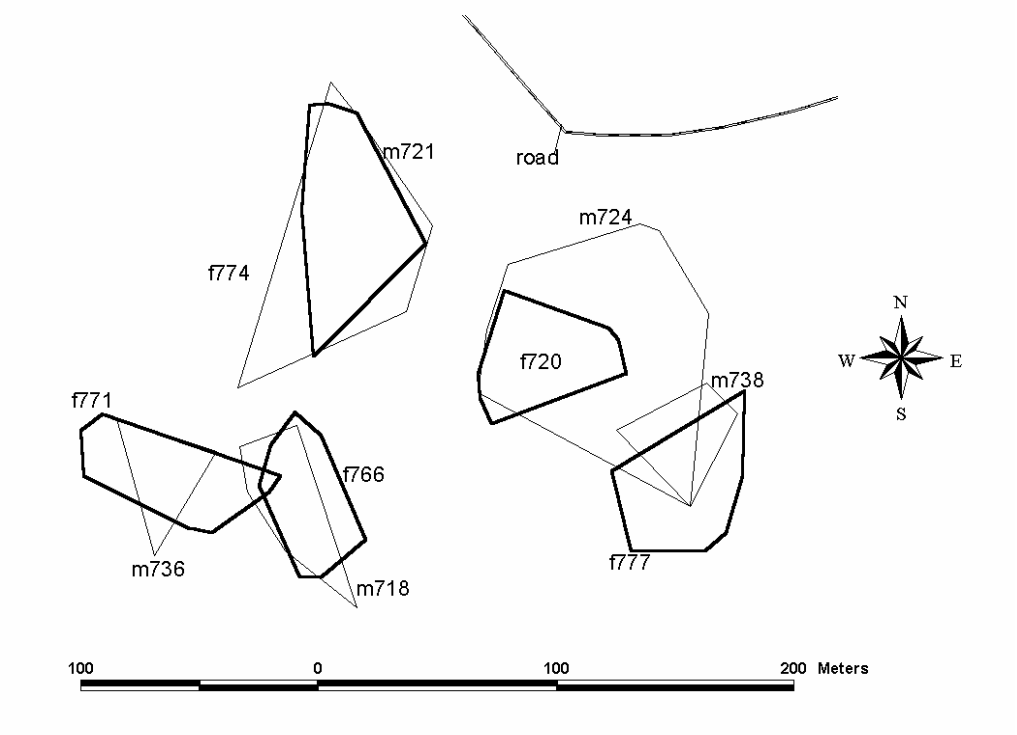

Fig. 2. – Minimum convex polygons of male (thin-lined polygons) and female (thick-lined polygons) *Elephantulus myurus* during November 2000.

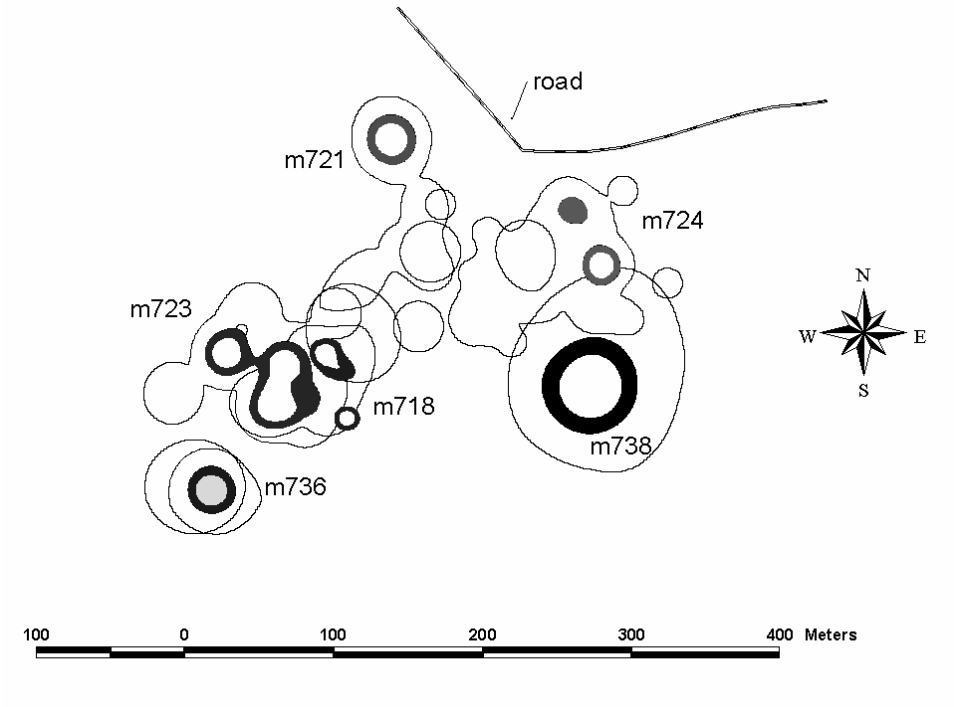

Fig. 3. – Density contours for the fixed-kernel-density estimates of males during the entire study. The thin-lined contours represent the 95% contours, and the thick-shaded contours represent the 50% contours.

Despite the cases where female ranges were overlapped by multiple males, each month there tended to be one primary male who 1) overlapped a majority of the female's range, and 2) consistently overlapped the female's home range during successive months. Based on these assertions, we assigned "putative" pairs each month (Table 1). It was apparent that when a male or female disappeared or died, another individual would quickly move

into or shift their home range to occupy the abandoned home range. For example, in October male 736 was adjacent to male 723 who was paired to female 771 (Table 1). In November, male 723 had disappeared and male 736 shifted his home range to coincide with female 771. In December, male 736 was found dead, likely due to predation. Another new male, 810, was trapped within the home range of female 771. Four cases of range shifts by adults were observed during this study, 3 by males and one by a female (Table 1).

Based on their locations when first observed, we identified offspring from 3 lactating females (Table 1). Two of these offspring, 783 and 784 (Table 1), were observed by flashlight around 2200 h one evening with their mother, female 766. While each of the 3 females were lactating we never observed any interactions between the lactating female and her presumptive mate, nor did we detect the two to be near each other with radiotelemetry.

At the end of the study, all trapping and radiotelemetry locations were combined to estimate the overall home-range size and intrasexual overlap. The fixed-kernel-density estimator (SEAMAN & POWELL, 1996) was also used to calculate home-range size using all the location data. The MCP estimates of home-range size using all data were significantly different between genders (male mean = 9901 $\pm$ 2593 m^2; female mean = 3623 $\pm$ 367 m^2; $P \leq 0.05$) and significantly larger than the monthly averages ($P \leq 0.05$ and $P \leq 0.01$ for males and females, respectively). The overall home-range size for males was 150% larger, whereas females were 80% larger than the monthly average. The 95% fixed-kernel estimates were also significantly larger for males (mean = 11065 $\pm$ 2576 m^2; Fig. 3) than females (mean = 3132 $\pm$ 220 m^2; $P \leq 0.05$). For males, the mean number of same-sex overlaps (3.7) and the mean percentage of intrasexual overlap (67%) were significantly greater for the overall combined data than the monthly averages for males ($P \leq 0.01$). There were no differences for females.

DISCUSSION

These data indicate that male and female *E. myurus* are spatially associated in monogamous pairs, yet males were never observed in the same vicinity of females with offspring supporting the presumption that males contributed no direct care to offspring. Similar results have been observed with other species of sengis, including *E. rufescens* (RATHBUN, 1979), *Rhynchocyon chrysopygus* (RATHBUN, 1979), *Petrodromus tetradactylus* (RATHBUN, 1979; FITZGIBBON, 1995), and *Macroscelides proboscides* (SAUER, 1973). These studies have led to the conclusion that all 15 species of Macroscelidea may be monogamous, making the sengis a very unique clade of mammals in which every species is monogamous. Why all sengis are monogamous is not clear.

There is no evidence that male sengis engage in any direct parental care activities, in part because the young are so precocial. Thus, it does not appear that direct male care explains monogamy in elephant-shrews. The benefits of the presence of the male to offspring survival and female reproductive success may be more subtle than the obvious direct benefits of male care of offspring. For example, males may defend a territory containing a female and her offspring that could increase resource availability (KLEIMAN, 1977; RUTHBERG, 1983), provide protection from infanticide (VAN SCHAIK & DUNBAR, 1990), and provide protection from predators (BARASH, 1975; DUNBAR & DUNBAR, 1980). Any of these factors could affect offspring and mother survivorship, and hence be a benefit to males in defending and mating with a solitary female. Sengis are very cursorial, often behaving more like small antelopes than typical small mammals (RATHBUN, 1984), and some species build and maintain elaborate networks of trails through the ground litter within their territories. RATHBUN, (1979) proposed that the trail-building activities of male *E. rufescens* (Rufous elephant-shrew) may indirectly benefit his female and offspring by providing efficient access to the territory for foraging and predator escape. Since *E. myurus* do not use trails, it is unlikely that females and their offspring benefit from trail maintenance activities, although there could be some other indirect benefits of the male's presence. It does seem clear, however, that the evolution of monogamy in *E. myurus* is not due to the necessity of male care (obligate monogamy).

In contrast to the necessity of male care in cases of obligate monogamy, facultative monogamy results when females exist at very low densities due to the dispersion and quality of food resources, and males can subsequently monopolize only one female (KLEIMAN, 1977, 1981; WITTENBERGER & TILSON, 1980; SLOBODCHIKOFF, 1984; BARLOW, 1988). The essential feature of facultative monogamy is that both sexes are constrained by resource quality and distribution so that monogamy is the only option available. If female ranges are widely dispersed, then individual males may only be able to access one female and mate monogamously.

If the density of females affects the strategies of males, a clear prediction of the facultative monogamy theory is that the mating strategies of males should be responsive to the density and availability of unpaired females. Recent studies of so-called facultatively monogamous species have indicated that males are not responsive to the availability of unpaired females (e.g. KOMERS, 1996), but rather males remain faithful due to the benefits of mate guarding. The evolutionary principle of mate guarding is that defending and mating with a single female during successive reproductive events is a better option than roving to mate with, or defending multiple females (PARKER, 1974; WITTENBERGER & TILSON, 1980; BROTHERTON & KOMERS, 2003). The benefits to mate guarding in mammals likely are due to the high costs of searching and or defending multiple females. Recently, mate guarding has been proposed to account for monogamy in *Madoqua kirkii* (Kirk's dik-dik). *M. kirkii* are socially and genetically monogamous (KRANZ, 1991; BROTHERTON et al., 1997), yet males exhibit no direct or indirect paternal behaviors that increase juvenile survivorship (BROTHERTON & RHODES, 1996). The dispersion of females does not appear to account for monogamy in this species either, as many males have territories large enough to encompass multiple females yet do not (BROTHERTON & MANSER, 1997), and mated males fail to respond to the presence of unmated females in adjacent territories (KOMERS, 1996). The reported costs to males of mating with multiple

females include increased predation, male-male competition, and the risk of being cuckolded by other males. Thus, the benefits of remaining with a single female and assuring access to one female during estrus outweigh the costs of mating with multiple females (KOMERS, 1996; BROTHERTON & MANSER, 1997). For females, it may be there are costs associated with harassment by extra-pair males, which results in females accepting monogamy (BROTHERTON et al., 1997).

Mate guarding may also explain the social organization of sengis. FITZGIBBON (1997) demonstrated that male *R. chrysopygus* that attempted to defend an additional female lost weight and could only temporarily defend the larger territory. This was presumably due to the costs of defending the extra female, not the extra space, as some males had territories twice the size of others (FITZGIBBON, 1997). In this study, monogamous associations of *E. myurus* persisted despite the fact that some males had home ranges large enough to encompass multiple females. The home ranges for the entire study were larger with more overlap in part due to an increase in sample locations over a longer time period. However, intrasexual overlap was significantly greater for males (67%) than females (18%; $P < 0.01$) for these home ranges. This indicates that over time, males have more variable and larger home ranges in which the boundaries are explored and expanded in different directions, supporting observations in other sengis that males make forays to monitor surrounding females (RATHBUN, 1979). There was likely competition for females, as range shifts were observed when male territory holders died or disappeared. It seems likely therefore, that this species is a model study organism in which to investigate the costs and benefits of mate guarding.

KOMERS & BROTHERTON (1997) argued that understanding the costs and benefits of defending solitary females, or mate guarding, may be the key issue to understanding the evolution of monogamy in mammals. Data from this study and other studies would further indicate that the monogamous members of the Macroscelidea are model organisms in which to experimentally manipulate the costs and benefits of defending solitary females and therefore advance our understanding of the evolution of monogamy in mammals in general.

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REFERENCES CITED

BARASH, D.P. (1975). Ecology of paternal behavior in the hoary marmot (*Marmota caligata*) : an evolutionary interpretation. *Journal of Mammalogy*, 56 : 613-618.

BARLOW, G. (1988). Monogamy in relation to resources. In : SLOBODCHIKOFF (ed), *The ecology of social behavior*. Academic Press, San Diego, CA : 55-79

BROTHERTON, P.N.M. & P.E. KOMERS (2003). Mate guarding and the evolution of monogamy in mammals. In : REICHARD & BOESCHE (eds), *Monogamy : Mating Strategies and Partnerships in Birds, Humans, and Other Mammals*, Cambridge University Press, Cambridge : 42-58.

BROTHERTON, P.N.M. & M.B. MANSER (1997). Female dispersion and the evolution of monogamy in the dik-dik. *Animal Behaviour*, 54 : 1413-1424.

BROTHERTON, P.N.M., J.M. PEMBERTON, P.E. KOMERS & G. MALARKY (1997). Genetic and behavioural evidence of monogamy in a mammal, Kirk's dik-dik (*Madoqua kirkii*). Proceedings of the Royal Society of London B, 264 : 675-681.

BROTHERTON, P.N.M. & A. RHODES (1996). Monogamy without biparental care in a dwarf antelope. Proceedings of the Royal Society of London B, 263 : 23-29.

CHURCHFIELD, S. (1987). A note on the diet of the rock elephant shrew, *Elephantulus myurus*, in Zimbabwe. *Journal of Zoology*, London, 213 : 743-745.

CORBET, G.B. & J. HANKS (1968). A revision of the elephant-shrews, Family Macroscelididae. *Bulletin of the British Museum of Natural History, Zoology Series*, 16 : 1-111.

DUNBAR, R.I.M. & P. DUNBAR (1980). The pairbond in the klipspringer. *Animal Behaviour*, 28 : 219-229.

DU TOIT, J.S. & L.J. FOURIE (1992). Bait preferences of the rock elephant shrew. *South African Journal of Wildlife Research*, 22 : 121-123.

FITZGIBBON, C.D. (1995). Comparative ecology of two elephant-shrew species in a Kenyan coastal forest. *Mammal Review*, 25 : 19-30.

FITZGIBBON, C.D. (1997). The adaptive significance of monogamy in the golden-rumped elephant-shrew. *Journal of Zoology*, London, 242 : 167-177.

HEDGES, S.B. (2001). Afrotheria : Plate tectonics meets genomics. Proceedings of the National Academy of Sciences, 98 : 1-2.

KERLEY, G.I.H. (1995). The round-eared elephant-shrew *Macroscelides proboscides* (Macroscelidea) as an omnivore. *Mammal Review*, 25 : 39-44.

KINGDON, J. (1997). *The Kingdon Field Guide to African Mammals*. Academic Press, London.

KLEIMAN, D.G. (1977). Monogamy in mammals. *The Quarterly Review of Biology*, 52 : 39-69.

KLEIMAN, D.G. & J. R. MALCOLM. (1981). The evolution of male parental investment in mammals. In : GUBERNICK & KLOPFER (eds), *Parental care in mammals*, Plenum Press, New York : 347-387.

KLEIMAN, D.G. (1981). Correlations among life history characteristics of mammalian species exhibiting two extreme forms of monogamy. In : ALEXANDER & TINKLE (eds), *Natural Sexual and Social Behaviour. Recent Research and New Theory*, Chiron Press, New York : 332-344

KOMERS, P.E. (1996). Obligate monogamy without paternal care in Kirk's dikdik. *Animal Behaviour*, 51 : 131-140.

KOMERS, P.E. & P.M.N. BROTHERTON (1997). Female space use is the best predictor of monogamy in mammals. Proceedings of the Royal Society of London B, 264 : 1261-1270.

KOONTZ, F.W., J.L. WELLINGTON & P.J. WELDON (1999). The sternal gland of the rufous elephant-shrew, *Elephantulus rufescens* (Macroscelidea, Mammalia) : anatomy, maturation, and secretion composition. In : JOHNSON, MULLER-SCHWARZE & SORENSON (eds) *Advances in Chemical Signals in Vertebrates*, Plenum Publishers, New York : 163-171.

KRANZ, K.R. (1991). Monogamy in the dik-dik. *Applied Animal Behaviour Science*, 29 : 87-105.

LUMPKIN, S. & F.W. KOONTZ (1986). Social and sexual behavior of the rufous elephant-shrew (*Elephantulus rufescens*) in captivity. *Journal of Mammalogy*, 67 : 112-119.

MURPHY, W.J., E. EIZIRIK, S.J. O'BRIEN, O. MADSEN, M. SCALLY, C.J. DOUADY, E. TEELING, O.A. RYDER, M.J. STANHOPE, W.W. DEJONG & M.S. SPRINGER (2001). Resolution of the early placental mammal radiation using Bayesian phylogenetics. *Science*, 294 : 2348-2351.

MZILIKAZI, N., B.G. LOVEGROVE & D.O. RIBBLE (2002). Exogenous passive heating during torpor arousal in free-ranging rock elephant-shrews, *Elephantulus myurus*. *Oecologia*, 133 : 307-314.

NEAL, B.R. (1995). The ecology and reproduction of the short-snouted elephant-shrew, *Elephantulus brachyrhyncus*, in Zimbabwe with a review of the reproductive ecology of the genus *Elephantulus*. *Mammal Review*, 25 : 51-60.

PARKER, G.A. (1974). Courtship persistence and female guarding as male time investment strategies. *Behaviour,* 48 : 157-184.

PERRIN, M.R. & C. TAOLO (1999a). Diet of introduced roan antelope at Weenen Nature Reserve, South Africa. *South African Journal of Wildlife Research,* 29 : 43-51.

PERRIN, M.R. & C. TAOLO (1999b). Habitat use by a herd of introduced roan antelope in KwaZulu-Natal, South Africa. *South African Journal of Wildlife Research*, 29 : 81-88.

RATHBUN, G.B. (1979). The social structure and ecology of elephant-shrews. *Advances in Ethology, Supplement to Journal of Comparative Ethology*, 20 : 1-77.

RATHBUN, G.B. (1984). Elephant-shrews, Order Macroscelidea. In : MACDONALD (ed), *The Encyclopedia of Mammals*. Facts on File Publications, New York : 730-735.

RUTHBERG, A.T. (1983). The evolution of monogamy in primates. *Journal of Theoretical Biology*, 104 : 93-112.

SAUER, E.G.F. (1973). Zum sozialverhalten der kurzohrigen elefantenspitzmaus, *Macroscelides proboscideus*. *Zetschrift fur Saugetierkunde*, 38 : 65-97.

SEAMAN, D.E. & R.A. POWELL (1996). An evaluation of the accuracy of kernal density estimators for home range analysis. *Ecology*, 77 : 2075-2085.

SLOBODCHIKOFF, C.N. (1984). Resources and the evolution of social behavior. In : PRICE, SLOBODCHIKOFF & GUAD (eds), *A New Ecology. Novel Approaches to Interactive Systems*, John Wiley and Sons, New York : 227-251.

STOCH, Z.G. (1954). The male genital system and reproductive cycle of *Elephantulus myurus jamesoni* (Chubb). *Philosophical Transactions of the Royal Society of London, B*, 238 : 99-126.

SWIHART, R.K. & N.A. SLADE (1985). Testing for independence of observations in animal movements. *Ecology*, 66 : 1176-1184.

TOLLIVER, D.K., L.W. ROBBINS, I.L. RAUTENBACH, D.A. SCHLITTER & C.G. COETZEE (1989). Biochemical systematics of elephant shrews from southern Africa. *Biochemical Systematics and Ecology*, 17 : 345-355.

VAN DER HORST, C.J. & J. GILLMAN (1941). The menstrual cycle in *Elephantulus*. *South African Journal of Medical Sciences*, 6 : 27-47.

VAN SCHAIK, C.P. & R.I.M. DUNBAR (1990). The evolution of monogamy in large primates : a new hypothesis and some crucial tests. *Behaviour*, 115 : 30-62.

WITTENBERGER, J.F. & R.L. TILSON (1980). The evolution of monogamy : hypotheses and evidence. *Annual Review of Ecology and Systematics*, 11 : 197-232.

WOODALL, P.F. & J.D. SKINNER (1989). Seasonality of reproduction in male rock elephant shrews, *Elephantulus myurus*. *Journal of Zoology*, London, 217 : 203-212.

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Density and cover preferences of Black-and-rufous elephant-shrews (*Rhynchocyon petersi*) in Chome Forest Reserve, Tanzania

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ABSTRACT. The objective of this study was to determine the density and habitat preference of the Black-and-rufous elephant-shrew (*Rhynchocyon petersi*) in Chome Forest Reserve, Tanzania. Chome Forest (143km^2) is located in the South Pare Mountains and provides critical habitat for endangered *R. petersi*. Twelve 300m transects were cut through the centre of the forest in an east-west direction and the number of elephant-shrew nests within 2.5 meters on each side of the transects was recorded. The mean number of nests per 100m transect (0.39 ± 0.47 [1SE]) translated to a density estimate of 19 elephant-shrews per km^2 (SE=23). Nest sites tended to be found in areas with greater than expected cover at the low (<5m) levels. These results indicate the population density of *R. petersi* is lower in the Chome Forest Reserve than in most populations in the Eastern Arc Mountains. The reasons for this difference and the conservation implications are discussed.

KEY WORDS : elephant-shrew, sengi, conservation, density.

INTRODUCTION

Africa's tropical forests are home to large diversity of species, many of which are endemic to the African continent. With increases in both human population and deforestation, more and more animals are becoming threatened (MYERS, 1988). The elephant-shrews or sengis (order Macroscelidea) are one such group. There are 15 species in this strictly African mammal group, three of which are referred to as "giant" elephant-shrews and are of the genus *Rhynchocyon* (Peters 1847). All three *Rhynchocyon* species are considered threatened due to habitat destruction and fragmentation, including the species that is the focus of this study, the Black-and-rufous elephant-shrew *(R. petersi*, Bocage 1880*)* (NICOLL & RATHBUN, 1990).

The giant elephant-shrews share similar life histories in that they are diurnal insectivores that live in lowland and montane forests and dense woodlands (RATHBUN, 1984). They can be found in altitudes ranging from sea level-2300m. While foraging they use their long proboscis to turn over leaf litter and dig up beetles, termites, other insects and centipedes. Once the arthropods are exposed, the sengi's long tongue extends and scoops them up (KINGDON, 1997).

For shelter, the giant elephant-shrews build nests. The dimensions of their shelters are typically one meter wide with a body-sized bowl of 20cm long, 15cm wide and 10cm deep (RATHBUN, 1979). Giant elephant-shrews live in monogamous pairs with defined territories and therefore each animal can make and maintain up to ten nests in one territory with several nests in use at one time (FITZGIBBON & RATHBUN, 1994). Their territories are typically about 1-1.7 hectare (RATHBUN, 1979). Because of their dependence on undisturbed forest and their large territories, their presence is an indication of a healthy forest ecosystem.

Of the giant elephant-shrews, the most is known about the Golden-rumped elephant-shrew (*R. chrysopygus*) and there are few records about *R. petersi*. The objective of this study was to estimate the density of elephant-shrews based on nest counts and analyze habitat preferences in an undisturbed forest reserve where *R. petersi* were known to occur (STANLEY et al., 1996).

MATERIALS & METHODS

Chome Forest Reserve is located within the Eastern Arc Mountains (37º 58' 0.12" E, 4º 17' 60" S), a range on the southeast coast of Kenya and the eastern coast of Tanzania. Chome Forest is made up of mostly wet montane forests (submontane, montane, and upper montane) with elfin forest on high ridges and heathlands on rocky, acidic soils. It covers approximately 142.8km^2 and is situated on the ridges and plateau of the South Pare Mountains in the district of Same in Kilimanjaro Region, Tanzania. The reserve was established in 1951 under the National Forest Policy and Draft Act to ensure ecosystem stability through conservation of forest biodiversity, water catchment and soil fertility. Because of the high annual rainfall and pristine forest cover, the forest has a high water catchment value and is an important resource for the 22 surrounding villages in the catchment area. The altitude in the reserve ranges from 1250-2400m. The estimated annual rainfall is 1400mm. During the dry season fire is a problem because it replaces dry and lower forests with heath land. Historically fire was not a threat but fires have increased with human activity near the forest. STANLEY et al. (1996) noted the presence of *R. petersi* in the Chome

Forest, but no study has documented the densities of these elephant-shrews in this forest.

This study was conducted in the rainy season between April 11th and 29th 2001. Chome Forest is accessible by road, but the forest itself is navigated only by footpaths. One such trail that is heavily trafficked bisects the middle of the forest from a west to east direction and is used by locals trekking from Mhero to Kanza or Mhero to Bombo. Because the path was established and because there had been sengi sightings in the area, this trail was chosen to be a reference path for transects. In order to estimate elephant-shrew density and habitat preference, transects were cut through the forest starting from the forest edge on the western side (near Mhero boundary). Twelve transects were cut perpendicular from the path, each 300m long and paced 500m apart. The first transect was 500m from the forest edge.

Nest frequencies within 2.5 meters on each side of the transect were tallied. Both newer (in use) and older nests were recorded. For more qualitative data, the number of scraping/digging sites was also tallied. Using a density conversion factor from FITZGIBBON & RATHBUN (1994) study on *R. chrysopygus*, the population density per km^2 was estimated.

To examine if giant elephant-shrews were selecting specific shade classes for their nests, percent canopy cover was estimated every 20m along each transect at each of three layers of canopy : $\leq$ 5m, 5-15m, and $\geq$ 15m. Percent canopy cover was divided into four shade classes, of 0-15%, 16-35%, 36-55% and >56%. Canopy cover was also recorded at each observed nest site and compared to available cover with χ^2 analysis.

RESULTS

The average number of nests found per 100m of transect was 0.39 (SE= 0.47). Using the density conversion factor from the FITZGIBBON & RATHBUN (1994) study, the estimated density was 19 per km^2 (SE=23). By extrapolation a liberal estimate for the whole reserve would be approximately 2700 *R. petersi*.

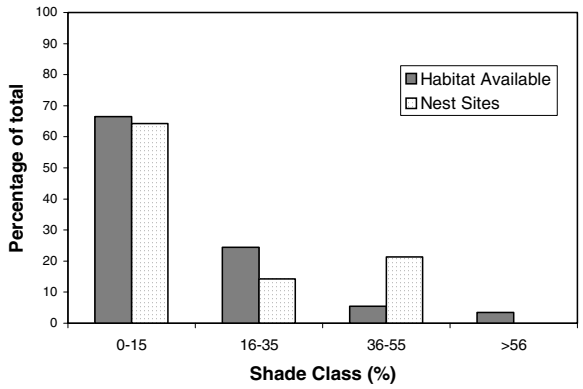

Fig. 1. – Shade classes for nest sites of *Rhynchocyon petersi* compared to the available habitat data collected every 20m.

There was no evidence that elephant-shrews were selecting specific shade classes in the middle or upper canopy layers (P > 0.10). However, in the lowest canopy layer (< 5m) elephant-shrews selected higher shade classes for nests than expected (χ^2 = 8.14, d.f.= 2, P < 0.05; Fig. 1). In particular the shade class of 36-55% was higher than expected (Fig. 1).

DISCUSSION

The estimated population of *R. petersi* in Chome Forest was 19 (SE=23) elephant-shrews per km^2. This estimate is most interesting when compared to density estimates of *R. petersi* from other forest reserves in the Eastern Arc Mountains. HANNA & ANDERSON (1994) estimated population density of *R. petersi* for seven study sites in the Eastern Arc Mountain range using similar techniques to this study (Table 1). The population density of Chome Forest Reserve is low when compared to these other sites where *R. petersi* was found. According to HANNA & ANDERSON (1994), the available habitat for *R. petersi* tends to be fragmented given its location at higher elevations, which is typically on isolated mountains. Current logging and hunting pressures on these forests have further exacerbated the lack of habitable areas for *R. petersi.* Though Chome Forest is closed to timber harvesting and hunting, pit saws and traps were sighted in the forest and therefore human activity in the forest could be limiting the numbers of *R. petersi*. Also because of the proximity of the village and the lack of a buffer zone, the forest is isolated which could prevent immigration into the existing population. FITZGIBBON (1994) suggested that for *R. chrysopygus* in Kenya, selective tree felling and pole cutting in protected areas have little effect on elephant-shrew densities but she warns that in unprotected areas, human pressure may be more of a threat.

TABLE 1

Estimated population densities of *Rhynchocyon petersi* in forest sites throughout Eastern Tanzania (from HANNAH & ANDERSON, 1994).

Forest site areas	Area (km^2)	Population density in pristine areas of forest reserve (No./ km^2)
Pugu	11	79.3
Kazimzumbwi	29	67.1
Ruvu	98	42.7
Kiono	20	42.7
Kisiju	2	0
Kwamkoro	Unknown	> 0 *
Kiwanda	Unknown	> 0 *
Chome – This study	143	19.0

* Not enough animals were captured for a density estimate, although a few animals were observed.

Rhynchocyon petersi chose nesting sites in areas of greater canopy cover than expected (Fig. 1), probably to avoid predators and to find sufficient leaf litter to construct nests. Nests were observed frequently at the base of trees, and typically wild coffee was the predominant shrub of the understory. Scraping and digging sites were often found near coarse woody debris perhaps due to the higher proportion of prey found living in this substrate. Finally, the forest edge seemed to have more nests (aver-

age of 2.7 nests/100m) than the other areas of the forest (0.3 nests/ 100m), indicating the Black-and-rufous elephant-shrew may perhaps forage in both the forest as well as in the surrounding heathland.

The population density conversion factor we used was determined from data collected on *R. chrysopygus* (FITZGIBBON & RATHBUN, 1994). HANNA & ANDERSON (1994) argued that *R. petersi* exist at lower densities than *R. chrysopygus*. If this is the case, then the conversion estimator results in a liberal density estimate for *R. petersi*. When extrapolating the population estimate for the entire forest, we assumed that the whole forest area provided adequate habitat for *R. petersi*, but there is evidence of disturbed areas of the forest which include burnings and heathland habitat which has not been known to support elephant-shrew nests. All of these surveys of *R. petersi* were conducted over short periods of time and ideally longer studies should be conducted. However, in general *Rhynchocyon* populations do not vary substantially over time (RATHBUN, 1979) so we are confident in our relative comparisons between forests.

The results of this study indicate that the population of *R. petersi* in Chome Forest Reserve is low and isolated when compared to other populations in the Eastern Arc Mountains and thus long term conservation plans must safeguard the future of the forest. This study also showed that forest cover is essential to the elephant-shrew, presumably to avoid predation, while leaf litter is crucial for nesting materials. With the proposed community conservation agreement and the re-opening of the forest to selective timber harvesting, the elephant-shrew population should be closely monitored.

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REFERENCES

FITZGIBBON, C.D. (1994). The distribution and abundance of the golden-rumped elephant- shrew *Rhynchocyon chrysopygus* in Kenyan coastal forests. *Biological Conservation,* 67 : 153-160.

FITZGIBBON, C.D. & G.B. RATHBUN (1994). Surveying *Rhynchocyon* elephant-shrews in tropical forest. *African Journal of Ecology,* 32 : 50-57.

KINGDON, J. (1997). *The Kingdon Field Guide to African Mammals*. Academic Press. San Diego, CA : 142-152.

HANNA, N. & J. ANDERSON (1994). Njule 92, Final Report, assessing the status and distribution of the black-and-rufous elephant-shrew. Unpublished report. Oxford University expedition to Tanzania. Oxford, England : 67pp.

MYERS, N. (1988). Tropical Forests and their Species : Going, going, …? In : WILSON (ed), *Biodiversity*. National Academy Press. Washington DC : 28-35.

NICOLL, M. & G. RATHBUN (1990). African Insectivora and Elephant-shrews : an action plan for their conservation. IUCN, Gland.

RATHBUN, G.B. (1979). The social structure and ecology of elephant-shrews. *Advances in Ethology, Supplement to Journal of Comparative Ethology*, 20 : 1-77.

RATHBUN, G. (1984). Elephant-shrews, Order Macroscelidea. In : MACDONALD (ed), *The Encyclopedia of Mammals*. Facts on File Publications, New York : 730-735.

STANLEY, W., S.M. GOODMAN & R. HUTTERER (1996). Notes on the insectivores and elephant shrews of the Chome Forest, South Pare Mountains, Tanzania. *Zoologische Abhandlungen*, 49 8 : 132-147.

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Evaluation of thiram and cinnamamide for protection of maize seeds against multimammate mice, *Mastomys natalensis*, in Tanzania

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ABSTRACT. Farmers in Tanzania consider rodents to be the major vertebrate pest of maize, especially at planting and seedling stages and annual losses are high. We evaluated the potential of two seed-dressing compounds, thiram and cinnamamide, as rodent repellents to protect maize against damage by multimammate rats, *Mastomys natalensis*. In laboratory tests, the two compounds showed a strong repellent effect against *M. natalensis* and thus the potential to protect maize seeds. The two compounds were evaluated in maize fields using Randomized Complete Block Design (RCBD) with three replications. The results show that these repellents are effective for protecting maize seeds against multimammate rats in the field, but in locations with high population of *Tatera leucogaster*, seedlings are still damaged after emergence. Therefore, in such locations, other control measures, including application of rodenticides just before seedling emergence may be necessary.

KEY WORDS : cinnamamide, economic loss, *Mastomys natalensis*, repellents, *Tatera leocogaster*, thiram, seed predation.

INTRODUCTION

In Tanzania, farmers consider rodents to be the main vertebrate pest (LEIRS et al., 2003). It has been estimated that the annual economic loss due to rodents in maize fields may amount to 42.5 million dollars (MULUNGU, 2003), a loss that may be preventable by poisoning and trapping (STENSETH et al., 2001). However, poisoning and trapping techniques are frequently ineffective, environmentally hazardous and socially unacceptable or uneconomic (MYLLYMÄKI, 1987). Thus alternative methods to prevent rodent damage are needed.

The deterrence approach to rodent control is not new (NOLTE & BARNETT, 2000, CAMPBELL & EVANS, 1985), although emphasis on chemical repellents as a means of reducing damage by rodents and other animals has increased in recent years. The need for materials to protect maize at planting and seedling stage is generally recognized (NGOWO et al., 2003). Ideal repellent seed dressing would prevent rodents from damaging the seed (SIMMS et al., 2000). The toxic effect on rodent should be minimal; otherwise they will act as rodenticides and basically create vacant space that will attract other rodents. Moreover, the repellents must not have phytotoxic effects that would reduce germination rates (NOLTE & BARNETT, 2000, MYLLYMÄKI, 1987, CAMPBELL & EVANS, 1985).

Preliminary laboratory studies from a wide range of botanic and synthetic repellents suggest that dressing maize seeds with thiram and cinnamamide can reduce damage to seeds by multimammate rats, *M. natalensis*. In general, repellents may be classified as either primary or secondary, according to their site of activity in the target species (ROGERS, 1978). Primary repellents provoke instantaneous responses through taste, olfaction, or irritation of the buccal cavity. Secondary repellents produce distressing effects after eating (e.g. gastrointestinal malaise or other illness) which, if associated with a novel cue, may cause the subject to develop a conditioned aversion to a given food (GILL et al., 1995). Some repellent compounds have both primary and secondary activity (GILL et al., 1994). For example, the cinnamamide used in the current study is considered bitter and does not smell good (GILL et al., 1995). Thiram has a bad strong smell which probably has olfactory repellence in rodents. The present study, therefore, reports the results of field tests with thiram and cinnamamide.

MATERIAL AND METHODS

Study locations

Two field experiments were conducted in December, 2002 and March, 2003 in Chunya (South -west Tanzania) and Mikese - Morogoro, (Eastern Central Tanzania), respectively, during the maize cropping seasons. In Chunya, maize is planted in November or December depending on the onset of rainfall, while in Mikese, it is planted in March. Initial trapping was carried out for three

consecutive nights one week before ploughing using 300 and 200 Sherman live traps per night at Mikese and Chunya, respectively, in order to determine the species composition and abundance. Therefore, there were a total of 900 and 600 trapping nights for Mikese and Chunya, respectively. The traps were placed in 100 x 100m grids, on 10 trap lines, 10m apart, each with 10 trapping stations also 10m apart. Peanut butter mixed with maize bran was used as bait. Traps were inspected each morning and captured animals were identified and counted according to species.

In both locations, the experimental set up was a Random Complete Block Design (RCBD) with three replications. The replicates were 70 * 70 m maize fields. Untreated seeds were planted in three control plots at each site. All plots were 100m apart. Other cultivated maize plots surrounded the experimental plots. In Chunya, only thiram was used to treat maize seeds. At Mikese, thiram and cinnamamide were used for seed dressing separately and each was, tested in three individual fields. Maize seeds (STAHA variety is commonly used by farmers in the study areas) not formally treated with chemicals (fresh from a farmer) were used in this study. Eighty grams of maize seeds were mixed thoroughly with 0.8 grams of the respective chemical repellent (i.e. thiram and cinnamamide). The treated seeds were left in the laboratory for 24 hours before planting and thereafter were planted in rows, 90cm apart and 60cm between planting holes, with three seeds per planting hole.

Assessment of crop damage

Crop damage assessment was carried out at seedling stage, 10 days after planting. We used a non-stratified systematic row sampling technique to assess damage as described by MWANJABE & LEIRS (1997) and MULUNGU et al. (2003). The sampling units were maize rows; four rows apart, leaving out the two outer rows. The assessor walked along maize rows across the plot, counting seedlings at each hole. Since three seeds had been planted per hole, we calculated the difference between observed and expected number of seedlings based on two assumptions, viz. the germination is 100% and other factors remain constant. The difference, therefore, was expressed as percentage damage.

Data Analysis

The data were analyzed in a general linear model with maize seed damage as the dependent variable and treatment as the factor interest, with field (and for thiram also site) as random factor (SAS, 1990). The damage data were subjected to Analysis of Variance (ANOVA) (SAS, 1990). The data were analyzed according to the following statistical model at each location :

$Y_{ij} = \mu + R_i + A_j + (RA)_{ij}$

Where :

Y_{ij} = Differences in maize seed damage

μ = Overall mean of maize seed damage

R_i = Replication effect

A_j = Treatment effect

$(RA)_{ij}$ = Experimental error

Since thiram was tested in both locations, the combined analysis was done by using the following model :

$Y_{ijk} = \mu + R_i + L_j + (RL)_{ij} + A_k + (LA)_{jk} + (RLA)_{ijk}$

Y_{ijk} = differences in maize seed damage due location different

μ = Overall mean of maize seed damage due to location difference

R_i = Replication effect

L_j = Location effect

$(RL)_{ij}$ = Main plot error

A_k = Treatment effect

$(LA)_{jk}$ = Location and treatment interaction effect

$(RLA)_{ijk}$ = Experimental error

RESULTS AND DISCUSSION

The effect of seed dressing on maize seed depredation at Mikese is shown in Table 1. The results show that there were highly significant differences ($F = 203.5$, $df = 2$, $p = 0.001$) between treated and untreated plots at Mikese : the treated maize seeds were less predated compared to untreated maize seeds. For Chunya, the results were not significantly different ($F = 1.42$, $df = 1$, $p = 0.36$) between treated and untreated maize seeds.

TABLE 1

The effect of dressing with Thiram and Cinnamamide on maize seed depredation by rodents in Mikese, Morogoro and Chunya, Mbeya, Tanzania

Treatments	Locations	
	Mikese	Chunya
Control	52.10 ± 3.51[a]	38.4 ± 9.03[a]
Thiram	27.53 ± 4.55[b]	46.8 ± 3.24[a]
Cinnamamide	26.41 ± 1.13[b]	-

Means followed by the same letter are not significantly different from one another at the 95% probability level.

In Chunya, the amount of rainfall was low and erratic, causing sporadic germination. During the evaluation, the distribution and amount of rainfall was an important factor that influenced rodent damage to maize seed germination (MULUNGU, 2003). Therefore, rodent damage to seeds and seedlings appeared to depend on the duration of germination, particularly in Chunya. Similar observations were reported by KEY (1990) on the effect of rainfall on maize damage by squirrels during the seedling stage. In areas with erratic rainfall germination is sporadic and hence, seeds and seedlings were available at intervals spreading over several days. We compared depredation of untreated seeds with maize seeds treated with thiram in Chunya and Mikese. The results show that depredation of untreated maize seeds at both locations did not differ significantly ($F = 5.05$, $df = 1$, $p = 0.09$), suggesting that the extent of rodent damage to untreated and treated seeds was similar. However, the interaction between treatment and location was significantly different ($F = 20.86$, $df = 1$, $p = 0.01$). This suggests that thiram treatment at Mikese was more effective in preventing rodent damage than at Chunya.

The differences between these two locations were probably due to the rodent species present. In Chunya, two rodent species, *Tatera leucogaster* and *M. natalensis*

TABLE 2

Rodent species composition at Mikese and Chunya (one week before planting).

Locations							
Mikese				Chunya			
Species	**Captured individuals**	**Trap nights**	**Composition (%)**	**Species**	**Captured individuals**	**Trap nights**	**Composition (%)**
Mastomys natalensis	688	900	98.01	*Mastomys natalensis*	287	600	93.79
Tatera leucogaster	10	900	1.42	*Tatera leucogaster*	19	600	6.21
Lemniscomysspp	4	900	0.57	-	-	-	-

were most abundant (Table 2) and both predated on maize seeds and seedlings. In this location, maize seedlings were cut, probably by *T. leucogaster*.

Similar observations were reported in India where *T. indica* caused damage to seedlings immediately after germination (RAO, A.M.K.M. personal communication). Therefore, in locations with high populations of *T. leucogaster* much higher damage will be expected in addition to that caused by *M. natalensis*. The initial trapping before planting indicated that the population of rodents at Mikese was dominated by *M.natalensis* (98%) while at Chunya, it was composed of *M. natalensis* (93%) and *T. leucogaster* (6%). Other species occurred in relatively low numbers. At Mikese, therefore, there were fewer depredations of seedlings in treated plots, most probably due to the absence of *T. leucogaster*. The discrepancies between these two locations suggest that it is unlikely that a single repellent will be effective against all seed and seedling depredating rodent species. The results suggest that thiram and cinnamamide are effective against *M. natalensis* after seedling emergence and that they can protect damage to maize seeds and seedlings in the absence of *T. leucogaster*.

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REFERENCES

CAMPBELL, D.L. & J. EVANS (1985). Evaluation of seedling protection materials for reducing wildlife damage on BLM lands in western Oregon : 1983 and 1984 : Olympia, Washington, *Report*.

GILL, E.L., R.W. WATKINS, J.E. GURNEY, J.D. BISHOP, C.J. FEARE, C.B. SCANLON & D.P. COWN (1995). Cinnamamide : A nonlethal chemical repellent for birds and mammals. In *:* MASON, J.R. (ed) *2nd Repellents in Wildlife Management Symposium : Proceedings of a Symposium*. Denver, Colorado, August 8-10 1995 : 43-51.

GILL, E.L., M.B. SERA, S.B. CANAVELLI, C.J. FEARE, M.E. ZACCAGNINI, A.K. NADIAN, M.L. HEFFERNAN & R.W. WATKINS (1994). Cinnamamide prevents captive chestnut-capped blackbirds from eating rice. *International journal of Pest Management*, 40(2) : 195-198.

LEIRS, H., A. SKONHOFT, N.C. STENSETH & H. ANDREASSEN (2003). A bioeconomics model for the management of *Mastomys natalensis* mice in maize fields. In : SINGLETON, G.R.; L.A. HINDS, C.J. KREBS & D.M. SPRATT (eds), *Rats, mice and people : Rodent biology and management*. ACIAR Monograph 96 : 358-361.

KEY, A. (1990). Pre-harvest crop losses to the African striped ground squirrel, *Xerus erythropus*, in Kenya. *Tropical Pest Management*. 36(3) : 223-229.

MULUNGU, L.S. (2003). Assessment of maize (*Zea mays* L.) damage and yield loss due to rodents in the field. *PhD* Thesis Sokoine University of Agriculture, Morogoro, Tanzania. 280pp.

MULUNGU, L.S., R.H. MAKUNDI & H. LEIRS (2003). Robustness of techniques for estimating rat damage and yield loss in maize fields. In : SINGLETON, G.R.; L.A. HINDS, C.J. KREBS & D.M. SPRATT (eds), *Rats, mice and people : Rodent biology and management*. ACIAR Monograph 96 : 224-228.

MWANJABE, P.S. & H. LEIRS (1997). An early warning system for IPM-Based rodent control in smallholder farming systems in Tanzania. *Belgian Journal of Zoology*, 127 : 49-58.

MYLLYMÄKI, A. (1987). Control of rodent problems by the use of rodenticides : rationale and constraints. In : RICHARDS, C.G.J. & T.Y. KU (eds), *Control of mammal pests*. Taylor & Francis, London. New York Philadelphia : 83-111.

NGOWO, V., J. LODAL; L.S. MULUNGU; H. LEIRS; R.H. MAKUNDI & A.W. MASSAWE (2003). Evaluation of Thiram and Cinnamamide as potential repellents against maize seed depredation in the field by the multimammate rat, *Mastomys natalensis*, in Tanzania. In : SINGLETON, G.R.; L.A. HINDS, C.J. KREBS & D.M. SPRATT (eds), *Rats, mice and people : Rodent biology and management*. ACIAR Monograph 96 : 260-261.

NOLTE, D.L. & J.P. BARNETT (2000). A repellent to reduce mouse damage to longleaf pine seed. *International Biodeterioration & Biodegradation*, 45 : 169-174.

ROGERS, J.B. (1978). Repellents to protect crops from vertebrate pests : some considerations for their use and development. *American Chemical Society Symposium Series*, 67 : 150-165.

SAS (1990). *SAS Statistics Users Guide, Statistical Analysis System*, Fifth ed. SAS Institute Inc. Carry, pp 1028.

SIMMS, L.C., C.E. MULLINS & M.J. WILSON (2000). Seed dressings to control slug damage in oilseed rape. *Project report* : pp22.

STENSETH, N.C.H., H. LEIRS, S. MERCELIS & P. MWANJABE (2001). Comparing strategies of controlling African pest rodents : an empirically based theoretical study. *Journal of Applied Ecology*, 38 : 1020-1031.

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Spatial patterns and distribution of damage in maize fields due to *mastomys natalensis* in Tanzania

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ABSTRACT. We describe the spatial distribution of rodent damage to maize seedlings in field studies in Morogoro, Tanzania. The distribution of damage was assessed at the level of the planting hole (with three seeds per planting hole) and at the level of the maize field (where the assessed units were plots of 10x10 planting holes). The most abundant rodent species in the fields were the multimammate rat, *Mastomys natalensis*. At the planting hole level, damage was fairly regular or random. At the field level, damage to seedlings was clustered irrespective of whether the fields were situated in mosaic or monoculture surroundings, but the clusters were not more concentrated near the edges or the near the centre of the field. We conclude that *M. natalensis* does not exhibit specific exhaustive searching behaviour when feeding on seeds and seedlings in maize fields and that several local factors determine the distribution of the damage.

KEY WORDS : *Mastomys natalensis*, spatial distribution, rodent damage, maize.

INTRODUCTION

Rodents have the potential to breed quickly and infest crops leading to serious economic damage (FIEDLER, 1994). In Tanzania, damage to maize crop is largely attributed to *Mastomys natalensis*, and the Nile rat, *Arvicanthis* sp. (MAKUNDI et al., 1991). In one study, more than 98% of the rodents found in maize fields were *M. natalensis* (MASSAWE et al., 2003). Little is known on the spatial distribution of the damage caused by *M. natalensis* in maize fields, although the spatial population patterns in Tanzania are known (LEIRS et al., 1996).

KEY (1990) and REDHEAD & SAUNDERS (1980) reported a strong correlation between rodent damage caused to maize and sugar cane and the presence of surrounding uncultivated land. BUCKLE et al. (1985) and SCHAEFER (1975) reported that at low population densities of *Rattus* sp., damage in rice fields was variable, sometimes clustered or sometimes evenly distributed over the field. At high population densities, the centre of the field was damaged, while border rows sustained little or no attack.

Proper sampling is essential for pest monitoring, surveillance and forecasting damage levels. Sampling methods have to be simple and unequivocal and must find a compromise between costs and desired precision (KRANZ, 1993). Sampling methods, sample size and sampling procedure, therefore, should be based on the spatial distribution of rodent damage in order to ensure that a sample is representative for the entire population in a particular field (APLIN et al., 2003). The aim of the current study was to describe the spatial distribution of rodent damage within maize fields in Tanzania, and establish whether these differ depending on the type of vegetation surrounding the fields.

MATERIALS AND METHODS

Locations and seasons

Field experiments were carried out during the cropping season of 2000 and 2001, in two farms at Sokoine University of Agriculture, Morogoro, Tanzania. The first farm is located at 6º50'S, 37º38'E at an altitude of 510 m above sea level (a.s.l.) and the second at 6º46'S, 37º37'E at 480 m a.s.l. The two areas have a bimodal rainfall pattern (with a long and a short rainy season). The study was conducted during the long rains which is also the main maize growing season. The seeds were sown in early March.

Treatments

The study was carried out in ten plots of 70 x 70 m each. Six of the maize fields were located in mosaic landscape of maize fields surrounded by fallow land; four were part of larger monoculture maize field. All fields received similar standard agronomic treatments, i.e. early ploughing, application of Triple Super Phosphate fertilizer (20 kg P_20_5/ha) before planting, and nitrogen fertilizer (40 kg N/ha) twice as a top dressing, three weeks after sowing and again after booting stage. Three maize seeds (of the local variety Staha®) were planted per hole, at a planting space of 90 x 60 cm between planting holes. Weeding was carried out twice.

Sampling procedures

Crop damage assessment was carried out at seedling stage, ten days after planting, by sampling every individual planting hole in each field. The assessor walked across the field and recorded the number of seedlings at each sampled hole in a row. Since three seeds were planted per hole, damage was expressed as the proportion of missing emerged seedlings. At this stage, there were no other pests causing damage to the seedlings and all missing seedlings were therefore attributed to rodent damage. Germination failure due to drought or seed quality was assumed to be evenly distributed, but was also considered of low importance in the experimental fields.

Determination of rodent damage distribution pattern

The variance-to-mean ratio (s^2/mean) of damage intensity at sampling points was calculated in order to estimate the distribution of rodent damage in each field. When the variance to mean ratio is large, the variation of damage distribution increases, meaning that damage is more aggregate. A small variance to mean ratio indicates a more regular damage distribution. KRANZ (1993) suggested that damage with a variance-to-mean ratio from 0.7 - 1.3 would be classified as random, with a ratio >1.3 aggregate or clustered and with a ratio <0.7 regular.

We analyzed the distribution of damage in the field at two levels. At a first level, the planting hole was used as the sampling unit. The number of missing seedlings was used as an indicator of damage at each planting hole. This could vary from 0 (indicating no seed removal by rodents) to 3 (indicating 3 seeds removed/damaged). A regular distribution at this sampling unit level would indicate that rodents removed an equal number of seeds from each planting hole, while a clustered distribution would mean that the damage was higher in some planting holes while others were left untouched. It should be pointed out that this level of analysis does not provide any information about the spatial distribution of damaged planting holes in relation to each other. For the second level of analysis, the field was divided into small areas of 10 x 10 planting holes. Damage was then calculated as the total number of missing seedlings in each area. An aggregate distribution at this level would indicate that seeds were removed or damaged in planting holes that are close to each other. A regular distribution would indicate that damage is spread uniformly over the field. At both sampling levels, the mean to variance ratio of damage was calculated for each field. Summary statistics of this ratio were then calculated for all fields in a mosaic landscape and for all fields in a monoculture landscape. The spatial distribution of damage was also plotted on a map to visually verify where in the field any clusters would occur.

RESULTS AND DISCUSION

The mean variance-to-mean ratios at the planting hole level were 0.5 and 0.8 in mosaic and monoculture fields, respectively (Table1). These results show a fairly regular distribution of damage in the mosaic fields and a more random distribution in the monoculture fields. However, with the larger sampling units (10 x 10 planting holes), the distribution of damage appeared to be highly clustered (variance–to-mean values of 3.6 and 3.7 for mosaic and monoculture fields, respectively), regardless of whether it was in mosaic or monoculture fields. Fig. 1 shows, as an example, a schematic representation of the spatial distribution of damage in one mosaic field. The nature of damage over the field can be readily seen, with areas of heavy damage and other areas with hardly any damage at all. However, the figure does not suggest clustering of damage in the centre or at the edges of the field. Maps for other fields show similar results.

TABLE 1

Variance to mean ratio and spatial distribution of rodent damage in Mosaic and Monoculture maize fields

	Field categories	
	Mosaic fields	**Monoculture fields**
	Individual planting hole	
Mean	0.49	0.83
Standard Error	0.03	0.07
Median	0.50	0.73
Minimum	0.39	0.70
Maximum	0.56	1.00
Confidence level (95.0%)	0.07	0.19
Number of fields (N)	6	4
	10 x 10 planting holes	
Mean	3.65	3.72
Standard Error	0.99	0.33
Median	3.70	3.73
Minimum	1.27	2.92
Maximum	7.90	4.52
Confidence level (95.0%)	2.55	1.04
Number of fields (N)	6	4

Scale used for variance : mean ratio; <0.7 = regular, 0.7 - 1.3 = random, and >1.3 = cluster. Adopted from KRANZ (1993).

The clustered distribution at the field level indicates that rodents are more active in some parts of the field than in others. This corresponds to observations that also rodent captures in those same fields are spatially clustered (MASSAWE, 2003). Small within-field variation in soil and vegetation cover may contribute to such clustering, and this could be affected by e.g. land preparation methods. As observed in another study, *M. natalensis* can adjust its feeding behaviour depending on prevailing local circumstances such as cover and predation risk (MOHR, 2001). Our study showed no obvious edge effect with more or, conversely, less damage near the field edges as observed in other crops with other rodent species (e.g. BUCKLE et al., 1985; SCHAEFER, 1975).

The random or regular distribution at the planting hole level is informative about the rodents' searching behaviour. The rodents do not necessarily dig up all seeds from single planting holes, rather they seem to move between planting holes without spending a long time searching at

each of them. In this way, the rodents may be actually thinning the seedling density but leaving one or more seedlings at each hole. As seen at the field level, however, such thinning is not done evenly throughout the field.

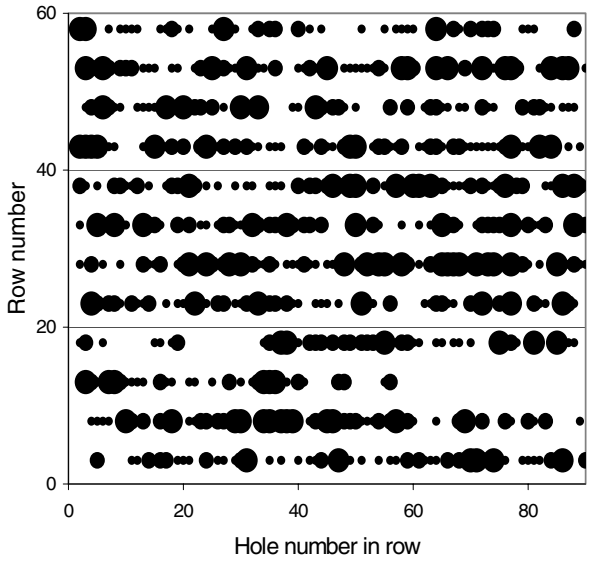

Fig. 1. – Spatial distribution of rodent damage along rows of a maize field in a mosaic landscape. Big bubbles indicate three seeds were removed by rodents, medium size bubbles indicate two seeds were removed, small bubbles indicate one seed removed, and no bubble (empty) indicates no seeds were removed. For clarity, we show on this figure only the observations for every 5th row, starting from row 3.

From our observations we conclude that *M. natalensis* does not exhibit specific exhaustive searching behaviour when feeding on seeds and seedlings in maize fields and that several local small-scale factors determine the distribution of the damage.

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REFERENCES

APLIN, K., P. BROWN, J. JACOB, C. KREBS & G. SINGLETON (2003). Field Methods for Rodent Studies in Asia and the Indo-Pacific. ACIAR Monograph, No.100 : 136pp.

BUCKLE, A.P., Y.C. YONG & H.A. RAHMAN (1985). Damage by rats to rice in South-east Asia with special reference to an integrated management scheme proposed for peninsular. *Acta Zoological Fennica*, 173 : 139-144.

FIEDLER, L. (1994). *Rodent Pest Management in East Africa*. Rome, Italy : 83pp.

KEY, A. (1990). Pre-harvest crop losses to the African striped ground squirrel, *Xerus erythropus*, in Kenya. *Tropical Pest Management*, 36(3) : 223-229.

KRANZ, J. (1993). Introduction to sampling in crop protection. In : KRANZ, J. & F. HOLZ (eds), *Basics of Decision - Making and planning for integrated pest management (IPM)*. Deutsche Stiftung für internationale Entwicklung (DSE), Federal Republic of Germany : 33-39.

LEIRS, H., W. VERHEYEN & R. VERHAGEN (1996). Spatial patterns in *Mastomys natalensis* in Tanzania (Rodentia, Muridae). *Mammalia*, 60(4) : 545-555.

MAKUNDI, R.H., T.J. MBISE & B.S. KILONZO (1991). Observations on the role of rodents in crop losses in Tanzania and control strategies. *Beitrage zur Tropischen Landwirtschaft und Veterinarmedizin (Journal of Tropical Agriculture and Veterinary Science)*, 29(4) : 465-474.

MASSAWE, A.W. (2003). Effect of cropping systems and land management practices on rodent population characteristics. PhD Thesis, Sokoine University of Agriculture, Morogoro, Tanzania : 176pp.

MASSAWE, A.W., H. LEIRS, W.P. RWAMUGIRA & R.H. MAKUNDI (2003). Effect of land preparation methods on spatial distribution of rodents in crop fields. In : SINGLETON, G.R., L.A. HINDS, C.J. KREBS & D.M. SPRATT (eds), *Rats, mice and people : Rodent biology and management*. ACIAR, Canberra : 229-232.

MOHR, K. (2001). Feeding decision as an anti-predation strategy in the African multimammate rat (*Mastomys natalensis*). MSc Thesis, University of Copenhagen, Denmark.

REDHEAD, T.D. & I.W. SAUNDERS (1980). Evaluation of thallium sulphate baits against rats in Queesland sugar-cane fields adjacent to different vegetation types. *Journal of Protection Ecology*, 2 : 1-19.

SCHAEFER, J. (1975). Field rat control as implemented by the Philippine-German crop protection program. In : *Proceedings of All India Rodent Seminar*. Ahmedabad, India : 345-351.

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Influence of land preparation methods and vegetation cover on population abundance of *Mastomys natalensis* in Morogoro, Tanzania

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ABSTRACT. A Capture-Mark-Release study was carried out in Morogoro, Tanzania, from April 1999 to April 2001 to investigate the effects of land preparation methods and cropping systems on population abundance of *Mastomys natalensis* in crop fields. Two land preparation methods (tractor ploughing; slash and burning) and two cropping systems (mono-cropping with maize; inter-cropping with maize and beans) were included in the study. The experimental design was a Complete Randomized Design with 2x2 factors, with two replicates. In slash and burn fields, rodent population abundance and distribution were strongly influenced by vegetation cover regardless of the type of cropping system. Higher rodent population peaks occurred in dense vegetation cover in slash and burn relative to tractor ploughed fields. In contrast, there were no obvious associations between vegetation cover and population abundance in the tractor ploughed fields, particularly in the mono-cropping system. A negative correlation between vegetation cover and population abundance of *M. natalensis* was obtained in fallow land surrounding the crop fields ($r = -0.63$; $p \leq 0.05$). The results show that the effect of vegetation cover on population abundance of *M natalensis* in crop fields is strongly influenced by the type of land preparation methods. Tractor ploughing and clearance of fallow land surrounding crop fields could be a useful method to reduce the invasion of crops by *M. natalensis*.

KEY WORDS : *Mastomys natalensis*, vegetation cover, land preparation methods, population abundance, Tanzania.

INTRODUCTION

Burning of vegetation in order to destroy rodent habitats has been a common practice in East Africa (GREEN & TAYLOR, 1975). In Tanzania, many farmers burn their fields in the aftermath of the harvest or immediately before ploughing. This probably changes the habitat for a short duration, but most likely it has no detrimental effect on the future population size of rodents because burnt areas soon have new vegetation and are re-invaded rapidly. The type of farming practices affects the nature of the habitat, shelter and population density of rodents (MAKUNDI et al., 1999). A mosaic of small plots of various crops, intermingled with patches of fallow and permanent grass-land, combined with minimum land preparation and subsequent flourishing of weeds, creates favourable conditions for rodents species especially *M. natalensis* and results in a high degree of damage (TAYLOR, 1968; MWANJABE, 1993; MYLLYMÄKI, 1989).

Little attempt has so far been made to determine interactions of rodents with the various cropping systems found in many agricultural areas under different land management practices (YEBOAH & AKYEAMPONG, 2001; WHISSON, 1996). One of these interactions, for example, is the influence of agricultural practices on certain ecological characteristics of rodent populations. In this study we tested the hypothesis that rodent population characteristics are influenced by land preparation methods and land management practices. Thus we investigated the relationship between rodent population abundance and vegetation cover in different cropping systems and land preparation methods.

MATERIALS AND METHODS

The study area was located at Solomon Mahlangu Campus (Mazimbu), Sokoine University of Agriculture, Morogoro, Tanzania (6°46'S 37°37'E, 480m above sea level). A capture-mark-recapture (CMR) study was conducted during the 1999 - 2000 cropping seasons. Eight 70x70m grids were prepared, consisting of 7 parallel lines, 10m apart, and 7 trapping stations per line (total of 49 trapping stations/grid), also 10m apart. One Sherman live trap was placed on each trapping station. A 200m-300m wide zone of fallow land separated the grids from each other. The grids were subjected to two types of cropping systems (mono-cropping and inter-cropping) and two land preparation methods (tractor ploughing; slash and burning). The mono-cropping system consisted of a monoculture of maize and the inter-crop consisted of a

mixture of maize and beans. The experimental design was a Completely Randomized Design (CRD) with 2x2 factors replicated twice. The grids were ploughed in November 1999 and February 2000 during the short and long rain seasons, respectively. Tractor ploughing was done using a disc plough at a depth of 30cm, a normal rooting depth for most annual crops. Slashing was done manually and the vegetation was left to dry and subsequently burned. Maize sowing followed a standard procedure (planting lines 90cm apart, plant holes 60cm apart, and three seeds per planting hole). The bean crop was sown 3 weeks after the maize, at a spacing of 50cm x 10cm. All necessary agronomic practices such as fertilizer application and weeding were carried out in all the plots. Triple Super Phosphate (20kg/ha) and Nitrogen (40kg N/ha) were applied before sowing and 3-4 weeks after sowing, respectively.

Trapping was conducted in each grid for three consecutive nights at intervals of four weeks. Traps were baited with peanut butter mixed with maize bran and were inspected early in the morning. Animals were marked by toe-clipping. The trapping station, sex, weight, and reproductive status of captured animals were recorded. Animals were later released at the station of capture. Plant cover estimations were done during the monthly capture session and were used to assess the effect of cover on population size. In each grid, the assessor moved diagonally across the grid from point 1A to 7G and from 1G to 7A. At each point a qualitative estimation of ground cover (other than maize crop) was made using a scale of 1-5, in quadrate measuring 5m*5m. The corresponding values were : 1 = no cover (< 15%); 2 = sparse cover (15-40%); 3 = moderate cover (41-65%); 4 = dense cover (66-90%); 5 = very dense cover (>90%). In the surrounding fallow land, cover estimation was done on all the four sides of the grids. The relationship between vegetation cover and rodent population abundance was investigated. Three parameters were used in the fittings : population size, vegetation cover in the field and vegetation cover in the fallow land. Correlation analysis was performed between the different factors using Pearson–moment product correlation. Population data were log transformed to normalize them before the analysis.

RESULTS AND DISCUSSION

The population dynamics of *M. natalensis* in the study area followed an already established pattern (TELFORD, 1989; LEIRS, 1995), but showed marked variations between individual fields brought about by land preparation methods and cropping systems. Slashing and burning, tractor ploughing, monoculture and intercropping resulted in differences in the habitats available to the rodents. Shelter and production of plant biomass were specifically altered by the land preparation methods. Slashing and burning took place in November and new vegetative growth occurred immediately after the onset of the short rains. This was followed by an increasing population size, probably due to an invasion from the fallow land (MERCELIS & LEIRS, 1999) and early breeding, which for *M. natalensis* occurs with the onset of short rains (LEIRS et al., 1993).

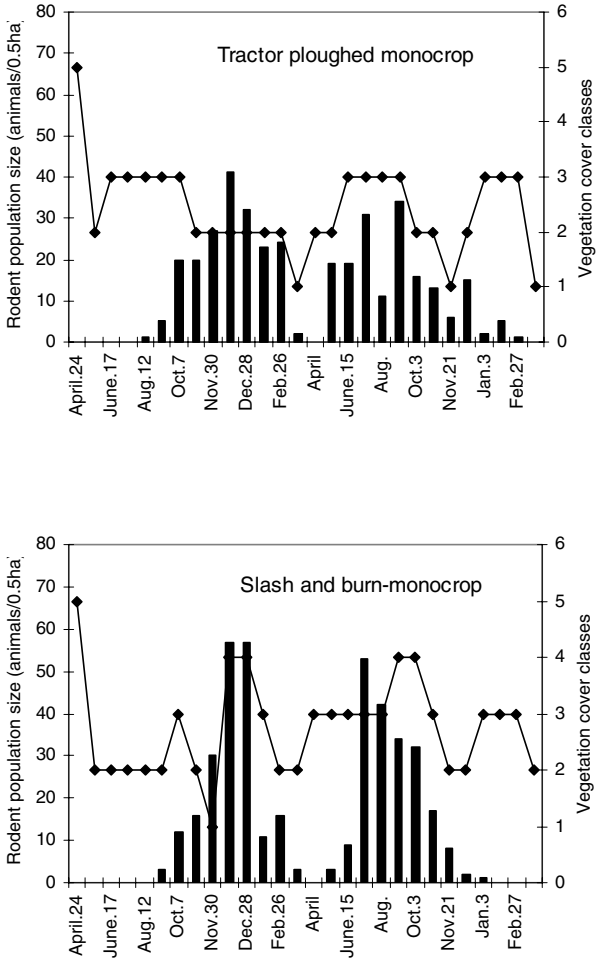

Fig. 1. – Rodent population abundance (bars) and vegetation cover (lines) in tractor ploughed fields (monocrop) and slash and burn fields (monocrop). Data were collected at intervals of four weeks.

Figs 1 and 2 show that higher population peaks were found in dense vegetation cover in slash and burn field than in the tractor ploughed fields. There was no obvious association between vegetation cover and population abundance in the tractor ploughed fields, particularly in the mono-crop. A negative correlation between vegetation cover and population abundance of *M. natalensis* was obtained in the fallow land (Pearson Product – Moment correlation; $r = - 0.63$, $p \leq 0.05$).

Population sizes increased with increasing cover in the slash and burn fields and decreasing cover in the fallow land ($r^2 = -0.62$; $p \leq 0.05$). In the tractor ploughed fields population size remained low as cover increased ($r^2 = - 0.51$; $p \leq 0.05$).

In the mono-cropped fields, rodent population size increased with decreasing cover in the fallow land ($N = 76$; $r^2 = - 0.54$; $p \leq 0.05$), while in the inter-cropped fields rodent population increased with decreasing cover in the fields. A high rodent population size occurred in the inter-cropped fields when cover was low. Seasonal variation in population size in relation to vegetation cover was observed. During the short rains and non-cropping season

(dry season), population size increased with increasing cover in the fields.

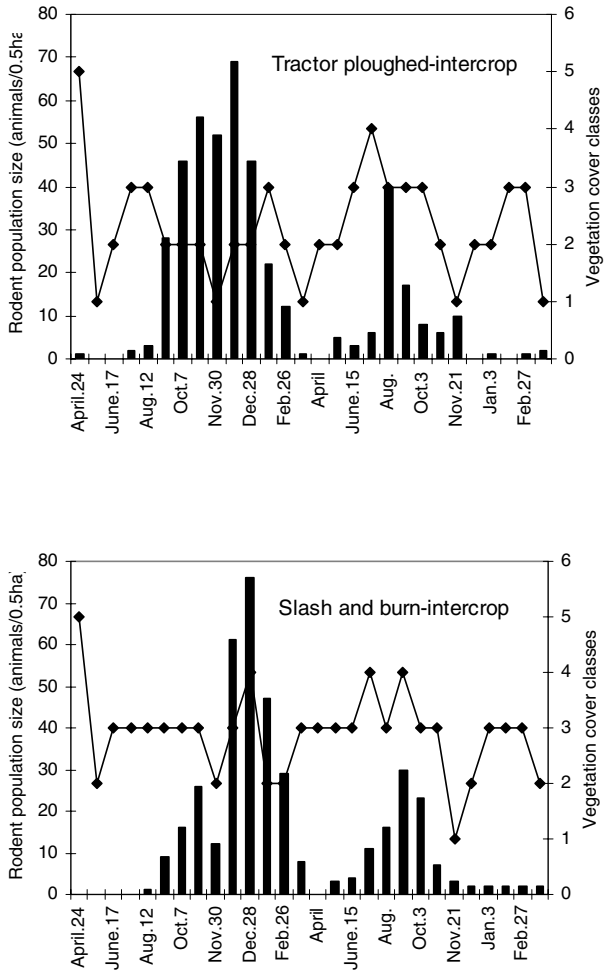

Fig. 2. – Rodent population abundance (bars) and vegetation cover (lines) in the tractor ploughed fields (intercrop) and slash and burn fields (intercrop). Data were collected at intervals of four weeks.

The selection for suitable habitat by *M. natalensis* is viewed to be a behavioural process, which maximizes fitness. Vegetation, apart from providing food resources, acts as cover for protection from predators. *M. natalensis* generally avoid exposed places to reduce the risks of predation (MOHR et al., 2003). The habitat changes were an important factor in the abundance of *M. natalensis* in the different fields. In crop fields, the changes are usually drastic and occur over a short period of time, which also brings about changes in the rodent population densities. The different types of treatments (tractor ploughed *versus* slash and burn and mono *versus* inter-crop) were associated with a sequence of habitat changes both temporally and spatially, and these are reflected in variation in the rodent population abundance in the different fields.

The fallow land with dense grass and weed cover became more and more unfavourable for *M. natalensis* particularly when new vegetation got established in the slash and burn and tractor ploughed fields. This is reflected in the negative correlation between cover and population abundance in the fallow land. MAKUNDI et al. (2000) reported that agriculture is a major disturbing factor in any ecosystem, and further commented that the timing and intensity of this activity may affect the species diversity and richness. This suggests that animals migrated from the fallow land to the crop fields and established new home ranges.

The opportunistic behaviour enables *M. natalensis* to take advantage of changes in habitats, particularly in relation to food resources. According to TAYLOR & GREEN (1976), when cereals and weed seeds were abundant, both grass and dicotyledonous plants (as found in the fallow land) were eaten sparingly or were absent in the diet of *M. natalensis*. It has been suggested that the fallow land at certain stages during the growth of the crop is a less suitable habitat compared to the crop fields.

It is apparent that agricultural activities may increase species richness (*M. natalensis*) whereas in the undisturbed fallow land the dominance of this species is reduced. This observation conforms to general theories in species succession (ODUM, 1971). In Australia, STICKEL (1979) reported that in a crop field – hay mosaic (analogous to crop –fallow land mosaic in our study area) the entire population of house mice moved from their long established home ranges in a hay field to a field of ripening wheat where they established new home ranges. Other studies have also shown the importance of farming practices on movements of populations of rodents. According to NEWSOME (1969a, b) the growth and harvest of wheat in Australia had major influence on the migration of house mice.

Our study shows a strong association between population size and vegetation cover in slash and burn fields. It is apparent that these fields were less disturbed than the tractor ploughed fields. This suggests that populations of *M. natalensis* build-up faster in slash and burn fields (mono and intercrop fields) than in the tractor ploughed fields probably due to higher survival and recruitment. Since the distribution of animals in the tractor ploughed fields was not random but was restricted to the edges (MASSAWE et al, 2003), it is an indication that there was less migration and colonization of these fields irrespective of the cover.

It is apparent that surrounding fallow lands in crop fields are an important consideration in rodent pest management. For example, studies in the Victoria Mallee, Australia, showed that fence-lines were the most important donor habitats because they provided abundant grass seed early in the breeding season (SINGLETON, 1989; TWIGG & KAY, 1994). Rodent management in such fields should aim at destruction of ground cover which affects rodents immediately by exposing them to predators and, more slowly, by removing their food supplies. Populations of *M. natalensis*, have been observed to increase after cover removal in adjacent fields (GREEN & TAYLOR, 1975). GREEN & TAYLOR (1975) therefore suggested that any attempts to reduce rodent numbers over wide areas by means of cover destruction would have to be coordinated so that all harbourage is removed at more or less the same time.

Our study also shows that following land preparation, animals escape into the fallow lands adjacent to crop

fields. Therefore, removal of the fallow patches and field sanitation measures, when conducted by all or the majority of farmers will reduce rodent population size in crop fields.

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REFERENCES

GREEN, M. & K.D. TAYLOR (1975). Preliminary experiments in habitat alteration as a means of controlling field rodents in Kenya. In *:* HANSSON, L. & B. NILSON, (eds), Biocontrol of rodents, *Ecological Bulletin*, 19 : 175-282.

LEIRS H., R.VERHAGEN & W.VERHEYEN (1993). Productivity of different generations in a population of *Mastomys natalensis* rats in Tanzania. *Oikos*, 68 : 53-60.

LEIRS, H. (1995). *Population ecology of Mastomys natalensis (Smith, 1834). Possible implication for rodent control in Africa*. Agricultural Edition No : 35. Belgium Administration for Development Cooperation, Brussels, 268pp.

MAKUNDI, R.H., N. OGUGE & P.S. MWANJABE (1999). Rodent pest management in East Africa - an ecological approach. In : SINGLETON, G.R., L.A. HINDS, H. LEIRS & Z. ZHIBIN, (eds), *Ecologically- based rodent management* (Edited by). ACIAR Monograph No. 59 : 460-476.

MAKUNDI, R.H., A. KALININ, A. PRZETAKIEWICZ & S.J. AHN (2000). Influence of land use on tenebroid beetle diversity. *Proceedings of the Third Mashav course on the conservation of Biodiversity in Desert Ecosystem*. May-June, 2000, University of Ben Gurion of the Negev : 97-107.

MASSAWE, A.W., H. LEIRS, W.P RWAMUGIRA & R.H. MAKUNDI (2003). Effect of land preparation methods on spatial distribution of rodents in crop fields. In : SINGLETON, G.R., L.A. HINDS, C.J KREBS & D.M SPRATT (eds), *Rats, Mice and People : Rodent Biology and Management*. Australian Centre for International Agriculture Research, Canberra : 229-232.

MERCELIS, S. & H. LEIRS (1999). The recolonization of "depopulated" maize fields by Rodent : implication for rodent control in Tanzania. *War against rats*, 8 : 11.

MOHR, K. (2003). Foraging of multimammate rats rat (*Mastomys natalensis*) under different predation pressure : cover, patch-dependent decisions and density-dependent GUDS. *Oikos*, 100 : 459-468.

MWANJABE, P.S. (1993). The role of weeds on population dynamics of *Mastomys natalensis* in Chunya (Lake Rukwa) valley. In : MACHANGU, R.S. (ed), *Economic importance and control of rodents in Tanzania*. Workshop proceedings, July 6-8, 1992, Sokoine University of Agriculture, Morogoro : 34-42.

MYLLYMÄKI, A. (1989). Population dynamics of *Mastomys natalensis* (Smith) in relation to agricultural systems, incidence of damage and implications in control strategies. *Final report*. Denmark-Tanzania Rodent control Project, DANIDA Mission- Dar-es-Salaam, Tanzania.

NEWSOME, A.E. (1969a). A population of house mice temporarily inhabiting a South Australian wheat fields. *Journal of Animal Ecology*, 38 : 341-360.

NEWSOME, A.E. (1969b). A population of house mice temporarily inhabiting a reedbed in South Australia. *Journal of Animal Ecology*, 38 : 361-377.

ODUM, E.P. (1971). *Fundamentals of Ecology* (3rd Edition). W.B. SAUNDERS Co. London. 574pp

SINGLETON, G.R. (1989). Population dynamics of an outbreak of house mice (*Mus domestica*) in the Mallee wheatlands of Australia-hypothesis of plague formation. *Journal of Zoology* (London), 219 : 495-515.

STICKEL, L.F. (1979). Population ecology of house mouse in unstable habitats. *Journal of Animal Ecology*, 48 : 871-188.

TAYLOR, K.D. (1968). An outbreak of rats in agricultural areas of Kenya in 1962. *East African Agricultural and Forestry Journal*, 34 : 66-77.

TAYLOR, K.D. & M.D. GREEN (1976). The influence of rainfall on diet and reproduction in four African rodent species. *Journal of Zoology, London*, 180 : 367-389.

TELFORD, S.R. (1989). Biology of the multimammate rat, *Praomys (Mastomys) natalensis* at Morogoro, Tanzania, 1981-1985. *Bulletin of Florida State Museum Biological Science*, 34(6) : 249-288.

TWIGG, L.E. & B.J. KAY (1994). The effect of microhabitat and weather on house Mouse (*Mus domestica*) numbers and the implications for management. *Journal of Applied Ecology*, 31 : 657-665.

WHISSON, D. (1996). The effect of two agricultural techniques on population of canefield rat (*Rattus sordidus*) in sugarcane crops of North Queensland. *Wildlife Research*, 23 : 589-604.

YEBOAH, S. & S. AKYEMPONG (2001). Factors influencing the distribution of the mole rat, *Crptomys zechi* (Rodentia, Bathyergidae) in Ghana. *African Journal of Ecology*, 39 : 233-240.

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Biodiversity and ecology of small mammals (Rodents and Shrews) of the "Réserve de Faune à Okapis", Democratic Republic of the Congo

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ABSTRACT. We carried out a small mammal (rodents and shrews) inventory in the Okapi Fauna Reserve in the Ituri Forest, Democratic Republic of Congo. Using snap traps and life traps we collected 1577 specimens of small mammals belonging to 7 species of Soricomorpha and 23 species of Rodentia. Rodents included *Hylomyscus parvus*, which previously only was known in D.R.Congo near Kisangani. The record of *Crocidura congobelgica* (Soricomorpha) is the second record after the description of the species.

Hybomys cf. lunaris (27.58%) and *Praomys jacksoni* (21.81%) were the most abundant and ubiquitous species on the prospected habitats (mixed forest, monodominant forest, swampy forest, hill forest, secondary forest and fallows) except in grassy fallows where *Lophuromys dudui* was the most abundant species. Other common species in the Reserve included *Deomys ferrugineus, Hylomyscus stella, H. aeta, Malacomys longipes* and *Praomys misonnei.* Shrews included *Crocidura congobelgica, C. hildegardeae, C. olivieri* and *Scutisorex somereni.* The Shannon-Wiener and Simpson diversity indices show a large diversity and high equitability in small mammal communities. The sex ratio for the principal species was near parity. All the species seemed to breed throughout the year but for most reproduction was less intensive in the dry season.

KEY WORDS : rodents, shrews, biodiversity, ecology, R.D. Congo, Réserve de Faune à Okapi.

INTRODUCTION

The biodiversity of the rainforest of Congo remains poorly documented. This is particularly true for small mammals. We carried out a study on small mammals (rodents and shrews) in the Réserve de Faune à Okapis, which is situated in the Ituri Forest, in the Northeast of the Democratic Republic of Congo. The Ituri forest (± 70000 km^2) and Epulu locality are well known as the main habitat of Okapi, *Okapia johnstoni* (Sclater, 1901). This forest also is the habitat of a diversity of other mammals, and one of the world's greatest diversity hotspots for forest ungulates (HART, 1985). The protection of the okapi's natural habitat led in 1992 to the establishment of a Natural Reserve named "Réserve de Faune à Okapis" here "RFO" (Fig. 1).

Since the middle of the 1980's, studies were undertaken in this forest in order to document the biodiversity as a basis for management (HART, 1985; HART, 1985; SIKUBWABO, 1987; KATEMBO, 1990; CONWAY, 1992; EWANGO, 1994; NDJANGO, 1994; TSHOMBE, 1994; MAKANA et al., 1998; MAKANA, 1999; HART & CARRICK, 1996; HART & BENGANA 1997). The present small mammal survey was carried out in July-August 1993 and March 1994.

Study areas

The RFO (13500 km^2) stretches from 1° to 3° N and 28° to more than 29° E. The elevation varies between 700 m a.s.l. in the extreme west and 1350 m on the highest rocky hills between the Epulu-Nepoko Rivers (HART & BENGANA, 1997).

Vegetation can roughly be classified as a mosaic of tropical rain forests including primary forest, swamps or marsh forests, fallows and secondary forests. Primary forests are mixed forests dominated by *Julbernadia seretii* and *Cynometra alexandri (Caesalpiniaceae*) and monodominant forests dominated by *Gilbertiodendron dewevrei* (Ceasalpiniaceae). Descriptions of these forests can be found in HART (1985), EWANGO (1994), NDJANGO (1994), MAKANA et al., (1995) and MAKANA (1999). There are no detailed climatic records for the RFO as a whole. However, BURTOT (1971) estimated the mean annual temperature as about 24 °C and annual rainfall between 1700 and 1800 mm. April, May, August and September are wettest while December, January and February receive less than 100 mm of precipitation. HART & CARRICK (1996) confirmed this climatic tendency in the research stations of Afarama, Epulu and Lenda (Fig. 2).

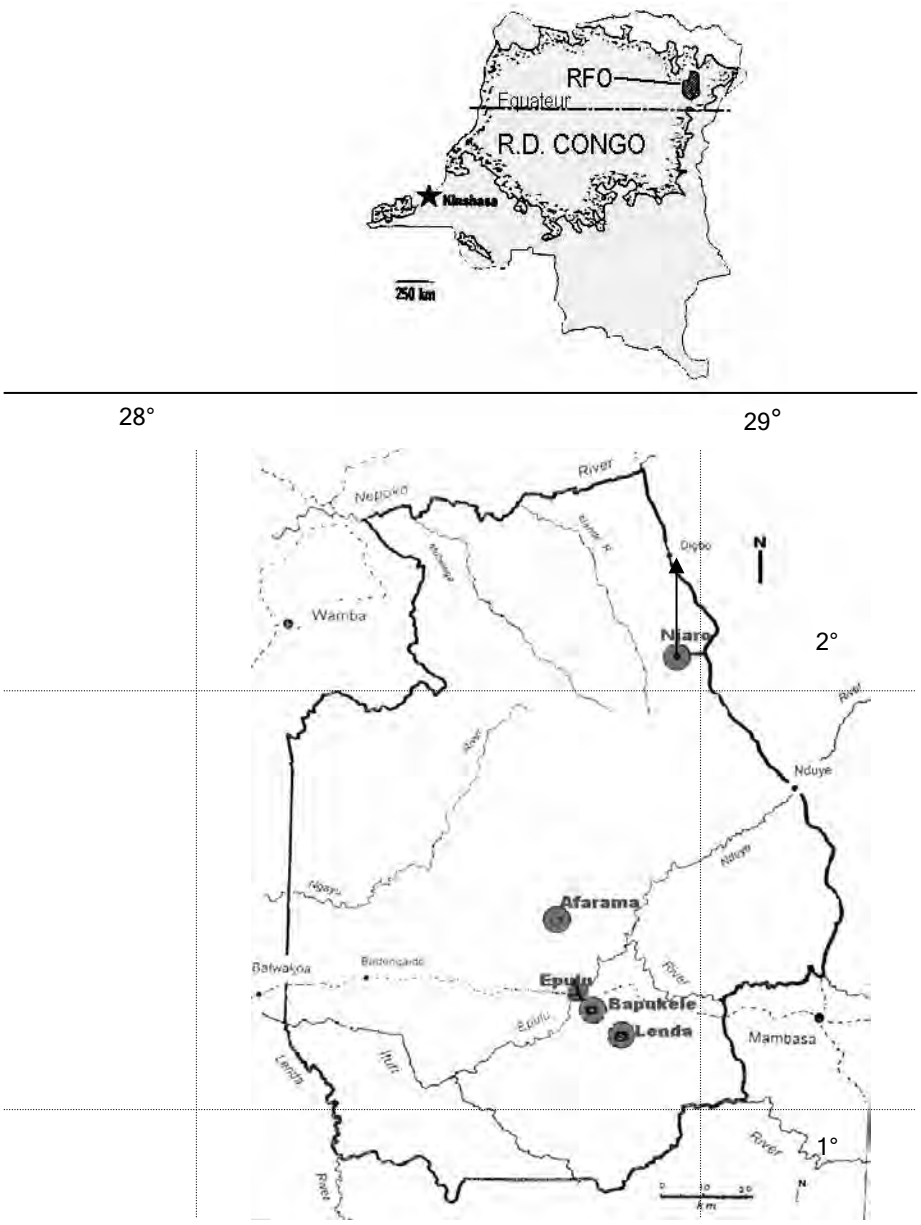

Fig. 1. – Map of the Réserve de Faune à Okapis, D.R.Congo, showing prospected localities (adapted from HART & BENGANA, 1997).

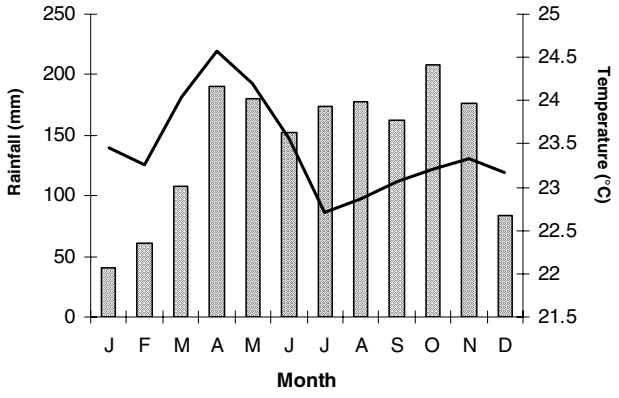

Fig. 2. – Annual variation of rainfall and temperature in RFO : Epulu sector (after data from HART & CARRICK, 1996).

MATERIAL AND METHODS

Small mammals were collected during two periods : 28 June to 8 August 1993 and 2 to 28 March 1994 in five localities : Afarama (AF) 1° 33' N, 28° 31' E, 800 m a.s.l.; Bapukele (BA) Epulu (EP) 1° 24'N, 28° 35 E, 760 m, Lenda (LE) 1°19' NS, 28° 38'E, 750 m and Njaro (NJ) 2°03'N, 28°50'E 960 m with Aketu hill 2° 5' N 28° 48' E, 1200 m.

Trap lines with trapping stations approximately 10 m apart were set following paths, trails, streams or small rivers. Three types of traps were used : Sherman LFA live traps, and "Victor" snap traps and "Museum Special" snap traps. Two traps baited with the pulp of palm nut (*Elaeis guinensis)* were placed at each trap station for tree consecutive nights. Traps were checked in the morning from 8 :30 am, and sometimes once again toward 5 :00 pm.

Each captured small mammal was preliminary identified, sexed, weighed and measured externally, sacrificed and then fixed in 10% formaldehyde solution. Identification and collection of reproductive condition data were completed in the laboratory. Diversity was evaluated with the Shannon-Wiener index, Simpson index and Equitability index. Local diversity indices were compared between localities using the sectoral index H_β (see KREBS, 1994; RAMADE, 1984).

RESULTS AND DISCUSSION

Species composition

We collected 1577 small mammals belonging to 30 species. The collection includes 33 shrews (2.09%, 7 species) and 1544 rodents (97.91%, 23 species). Seven shrew species were caught. The most common species are *Crocidura denti* (0.57%) and *C. olivieri* (0.44%). The record of *C. congobelgica* is the second record after the description of the species in 1916 (HOLLISTER, 1916). Shrew diversity in RFO seems to be poorer than in Masako Reserve (12 species) (DUDU, 1991). This might be due to the short survey period of our study and the use of Victor and Museum Special snap traps that are not very appropriate to catch shrews.

Among the rodents four groups occur. Dominant species *Hybomys cf lunaris* (27.58%), *Praomys jacksoni* (21.81%) and *Hylomyscus stella* (13.25%) represent together 62.65% of all rodent specimens. Moderately abundant species *Praomys misonnei* (6.53%), *Malacomys longipes* (5.96%) *Hylomyscus aeta* (5.77%), *Deomys ferrugineus* (5.07%) and *Lophuromys dudui* (4.57%) total 27.90%. Occasional species *Mus minutoides* and *Lophuromys luteogaster* with respectively 2.28% and 1.84%. The last group includes twenty rare species (<1% each) that together total only 5.33% of all specimens. Among the rare species we found *Hylomyscus parvus,* which grants RFO the status of being the second site in D.R. Congo where *H. parvus* is recorded, the first site being Masako near Kisangani. Other noteworthy rare species are *Dendromus mystacalis, Graphiurus lorraineus, Colomys goslingi* and *Praomys verschureni.* With 23 species recorded, the rodent species diversity in RFO seems to be high and comparable to of the other forest blocks in the Congo-basin. RAHM (1966) and DUDU (1991) mentioned 26 and 28 species respectively for Irangi and Masako. Around Kisangani, new data (MUKINZI et al., 2003) counted 30 species. The number of species in the RFO, reported here, is only a minimum value and could increase by surveys that are extended time and space, by including species that we have seen but not caught, as well as species reported by other authors as HATT (1940) and CARPANETO & GERMI, (1989). These species are *Thryomomys swinderianus, Atherurus africanus, Anomalurops beecrofti, Anomalurus derbianus, A. pusillus, Idiurus macrotis* and *l. zenkeri; Funisciurus pyrrhopus, F. alexandri, Heliosciurus rufobrachiu,* and *Protoxerus stangeri.*

TABLE 1

Number of specimens collected for different species in the Réserve de Faune à Okapis, DR Congo, in 1993 and 1994. The lower part of the table indicates a number of diversity indices.

Species	1993	1994	Total
Soricomorpha			
Crocidura congobelgica Hollister, 1916	3	1	4
Crocidura denti Dollman, 1915	3	6	9
Crocidura hildegardeae Thomas, 1904	-	3	3
Crocidura latona Hollister, 1918	1	2	3
Crocidura olivieri (Lesson, 1827)	4	3	7
Crocidura sp.	2	2	
Scutisorex somereni (Thomas, 1910)	2	2	4
Rodentia	-	-	
Colomys goslingi Thomas & Wroughton, 1907	-	2	2
Cricetomys emini Wroughton, 1910	-	1	1
Dendromus mystacalis Heuglin, 1863	-	1	1
Deomys ferrugineus Thomas, 1888	44	36	80
Funisciurus anerythrus (Thomas, 1890)	2	1	3
Grammomys kuru	1	2	3
Graphiurus lorraineus Dollman, 1910	1	-	1
Hybomys cf. lunaris Thomas, 1906	173	262	435
Hylomyscus aeta (Thomas, 1911)	75	16	91
Hylomyscus parvus Brosset et al.,1965	-	1	1
Hylomyscus stella (Thomas, 1911)	88	121	209
Lemniscomys striatus (Linnaeus, 1758)	2	6	8
Lophuromys dudui Verheyen et al., 2002	39	33	7
Lophuromys luteogaster Hatt, 1934	4	25	29
Malacomys longipes Milne-Edwards, 1877	46	48	94
Mus minutoides A. Smith, 1834	5	31	36
Oenomys hypoxanthus (Pucheran, 1855)	1	9	10
Paraxerus boehmi (Reichenow, 1886)	1	5	6
Praomys jacksoni (De Winton, 1897)	118	226	344
Praomys misonnei Van der Straeten & Dieterlen, 1987	57	46	103
Praomys verschureni (Verheyen & Van der Straeten, 1977)	1	2	3
Rattus rattus (Linnaeus, 1758)	-	3	3
Stochomys longicaudatus (Thomas, 1915)	6	4	10
Number of specimens	677	900	1577
Number of species	23	29	30
Shannon-Weiner diversity index H_α	3.161	3.121	3.205

TABLE 1

Number of specimens collected for different species in the Réserve de Faune à Okapis, DR Congo, in 1993 and 1994. The lower part of the table indicates a number of diversity indices.

Species	1993	1994	Total
H_α maximum (Hmax)	4.523	4.858	4.907
Equitability (E)	0.698	0.643	0.653
Simpson diversity index (D)	0.855	0.823	0.800
Sectoral index H_β			0.063

A lower number of species was recorded in at Afarama (11) and Lenda (12) where undisturbed primary forests prevail than in Bapukele (16), Epulu (22) and Njaro (24) where the regenerating habitats (fallows and secondary forest) are common. Indeed, in these anthropogenous environments, crops and rich herbaceous stratum provide small mammals with food and necessary shelter as suggested by DIETERLEN (1989) and DUDU (1991).

The community of small mammals in the localities of the RFO is much diversified : H_α = 2.766; 2.779; 3.018; 3.054; 3.156; and D = 0.843; 0.825; 0.799; 0.818; and 0.838 and E = 0.800; 0.775; 0.684; 0.671; and 0.789 respectively for Afarama, Lenda, Epulu, Njaro, and Bapukele. The same species are encountered in different localities and habitats as shown by the Shannon-Wiener sectoral index (H_β). In all pairs of localities, H_β approaches zero, indicating very strong similarity between the localities (RAMADE, 1984) (the lowest value was 0.026 for Bapukele-Epulu and the highest value 0.233 for Afarama-Epulu) (Fig. 3).

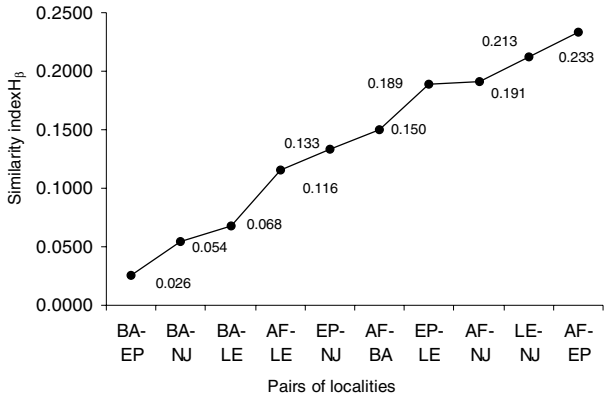

Fig. 3. – Pairwise similarity between trapping localities in the Réserve de Faune à Okapis, D.R.Congo

Sex ratio

The sex ratio (males/females) of 13 main species was not far from parity (Table 2). However, in most species a slight advantage in favour of males was observed. Our results are similar to those obtained by DUDU (1991) and DUDU et al. (1997) in Masako Reserve.

Reproduction

Reproduction occurred in both trapping periods (seasons) although it seems more intensive in the wet season. All three age classes (juveniles, sub-adults and adults) were present in the wet and dry seasons. The percentage of pregnant females varied between 25 and 62%. In the wet season, there were 28 to 81% pregnant females, whereas in dry season this percentage declined slightly (23 to 55%) according to the species (Fig. 4).

TABLE 2

Sex ratio of the most common species Réserve de Faune à Okapis (RFO, this study) and Masako Reserve (DUDU, 1991)

Species	RFO			Masako
	F	M	M/F	M/F
Deomys ferrugineus	33	41	0.80	0.67
Hybomys cf. lunaris	196	231	0.85	0.98
Hylomyscus aeta	50	41	1.22	-
Hylomyscus stella	81	122	0.66	0.47
Lophuromys dudui	34	38	0.89	0.85
Lophuromys luteogaster	13	11	1.18	-
Malacomys longipes	46	47	0.98	1.15
Mus minutoides	12	11	1.09	-
Oenomys hypoxanthus	5	3	1.67	-
Paraxerus boehmi	1	5	0.20	-
Praomys jacksoni	143	186	0.77	0.70
Praomys misonnei	38	64	0.59	-
Stochomys longicaudatus	5	5	1.00	1.08

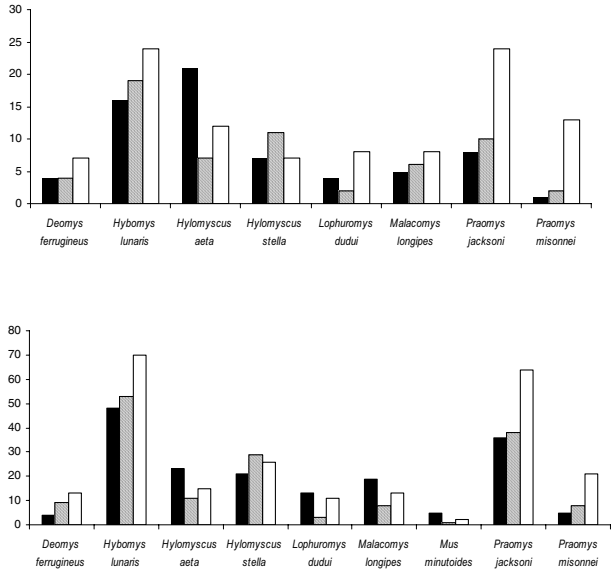

Fig. 4. – Proportion of female reproductive classes in common species during the wet season (upper graph) and the dry season (lower graph) in the Réserve de Faune à Okapis, D.R.Congo. Black columns = juveniles, barred columns = adults, white columns = pregnant.

The presence of sexually active individuals in each trapping session is an indication of reproductive activity

during the wet and the dry season. Several authors reported that the reproduction activity of small mammals in the tropical rain forest is continuous throughout the year, but with peaks in the wet season and throughs in dry season (RAHM, 1970; DUBOST, 1968; DIETERLEN, 1986; DUPLANTIER, 1989; DUDU, 1991). In the RFO, food resources are always available during the course of the year (HART, 1985) and breeding activity can take place in all seasons, but is still linked to the seasonal rainfall distribution (Fig. 2). This resembles the observations of DUBOST (1968) in Gabon, HAPPOLD (1977, 1978) in the Nigeria rain forest, and DUDU (1991) in Masako Reserve (RD Congo).

Litter size

The litter size (Table 3) is generally small (1-4 embryos) with the average that varies in the same range as reported by RAHM (1970) HAPPOLD (1978) DIETERLEN (1989) and DUDU (1991) for the same species.

TABLE 3

Observed litter sizes of some common rodent species in the Réserve de Faune à Okapis, D.R. Congo. N=sample size; Max=maximum observed litter size; Avg=average observed litter size; Literature=reported values for this species in literature

Species	N	Max	Avg	Literature
Deomys ferrugineus	12	3	1.84	1.69
Hybomys cf. lunaris	74	4	2.24	2.02-2.8
Hylomyscus aeta	14	4	3.14	2.9-3.4
Hylomyscus stella	25	4	3.00	-
Lophuromys dudui	11	3	2.50	1.83-3.0
Malacomys longipes	13	4	2.30	2.5-3.19
Praomys jacksoni	65	4	3.06	2.19-3.8
Praomys misonnei	20	4	3.15	-

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REFERENCES

BULTOT, F. (1971). Atlas climatique du basin congolais. Publications de l'institut pour l'Etude Agronomique au Congo (I.N.E.A.C.). Hors série.

CARPANETO, G.M. & F.P. GERMI (1989). The mammals in the zoological culture of the Mbuti Pygmies in North-Eastern Zaire. Hystrix (n.s.) 1 : 1-83.

CONWAY, D. (1992). A comparison of soil parameters in monodominant and mixed forest in Ituri forest, Zaire. University of Aberdeen Tropical environment Science. Honour Project, Scotland.

DIETERLEN, F. (1986). Seasonal reproduction and population dynamics in Rodents of an African Lowland rain forest. *Cimbebasia,* Ser (A), 8 H (1) : 1-7.

DIETERLEN, F. (1989). Rodents. In : LIETH, H. & M.J.A. WERGER (ed), *Tropical Rain Forest Ecosystems.* Elsevier Science : 383-400.

DUBOST, G. (1968). Aperçu sur le rythme annuel de reproduction des Muridés du Nord-Est du Gabon. *Biol. Gabonica,* 4 : 227-239.

DUDU, A.M. (1991). Etude du peuplement d'Insectivores et de Rongeurs de la Forêt ombrophile de basse altitude au Zaire (Kisangani, Masako). Unpublished Ph.D. thesis, Antwerpen University.

DUDU, A., R.VERHAGEN, H. GEVAERTS & W. VERHEYEN (1997). Population structure and reproductive cycle of *Praomys jacksoni* (De Winton, 1897) and first data on the reproduction of *P. misonnei* Van der Straeten & Dieterlen, 1987 and *P. mutoni* Van der Straeten & Dudu, 1990 (Muridae) from Masako forest (Kisangani, Zaire). *Belg. J. Zool.,* 127 (suppl. 1) : 67-70.

DUPLANTIER, J.M. (1989). Les rongeurs myomorphes forestiers du Nord-Est du Gabon : Structure du peuplement, démographie, domaines vitaux. Rev. *Ecol (Terre et Vie),* 44 : 329-346.

EWANGO, N.E. (1994). Contribution à l'étude structurale de la fôret monodominante à *Gilbertdendron dewevrei* de la Réserve de Faune à Okapi (Ituri, haut-Zaïre). Mémoire de licence inédit, 66 p. & annexes.

HAPPOLD, D.C.D. (1977). A population study on small Rodents in tropical rain forest of Nigeria. *Terre et la Vie*, 31 : 385–458.

HAPPOLD, D.C.D. (1978). Reproduction, growth and develop of a West African mouse, *Praomys tullbergi* (Thomas). *Mammalia*, 42 : 73-95.

HART, J. & P. CARRICK (1996). Climate of the Réserve de Faune à Okapis : Rainfall and temperature in the Epulu sector 1986-1996. CEFRECOF Working paper n° 2.

HART, J.A. & F. BENGANA (1997). Distribution and status of large Mammals and Human activities in the Réserve de Faune à Okaps, Démocratic Replublic of Congo. Summary Report with Recommendations for Conservation zoning and managment; 14 p + fig.

HART, J.A. (1985). Comparative dietary ecology of a community of frugivorous forest ungulates in Zaire. Ph.D. thesis, Michigan State University : 170 p.

HART, T.B. (1985). The ecology of a single-species dominant forest and a mixed forest in Zaïre, Africa. Ph.D. thesis, Michigan State University : 215 p.

HATT, R.T. (1940). Lagomorpha and Rodentia other than Sciuridae, Anomaluridae and Idiuridae, collected by the American Museum Congo Expedition. *Bull. Am. Nat. Hist.,* 76 : 457–604.

HOLLISTER, N. (1916). Shrews collected by the Congo expedition of the Amecican Museum. *Bull. Amer. Nat. Hist.,* 35 : 663-680.

KREBS, C.J. (1994). Ecology. The Experimental Analysis of Distribution and abundance. 4th edition, Harper Collins College Publishers. 801 p.

KATEMBO, M. (1990). Contribution à l'étude du régime alimentaire du léopard *Panthera pardus* (Linnée, 1758), Carnivora dans la forêt de l'Ituri (Zaire). Mémoire de licence, UNIKIS.

MAKANA, J.R., T. HART & J. HART (1995). Forest structure and diversity of liana and understory treelets in monodoninant and nixed forest in the Ituri Zaire. SI/MAB Symposium : 23-25.

MAKANA, J.R. (1999). Forest structure, species diversity and spatial patterns of trees in monodominant and mixed forests strands in the Ituri forest, Democratic Republic of Congo. MS thesis, Oregon State University.

MAKANA, J.R., T. HART & J. HART (1998). Forest structure and diversity of liana and understory treelets in monodoninant and nixed forest in the Ituri, Zaire. In : DALLMEIER F. & J.A. COMISKEY (eds), *Forest biodiversity research, Monitoring and Modeling. Conceptual Background and old World Case*

studies. Vol. 20, Man and Biosphere Series. The Parthenon Publishing Group, Pearl River, N.Y. : 429-446.

Mukinzi, I., N. Kadange, A. Bapeamoni, D. Amundala, T. Gembu, K. Kaswera, M. Danadu, M. Gambalemoke, P.G.B. Katuala, M. Colyn, R. Hutterer & A. Dudu (2003). Preliminary data on rodents and shrews (Mammalia) biodiversity in the Kisangani periphery. 9th International African Small Mammals *Symposium*, Sokoine University of agriculture, Morogoro, Tanzania. *Abstracts* : p 56.

Ndjango, N. (1994). Contribution à l'étude de la forêt mixte de la Réserve de Faune à Okapi (Ituri, Haut-Zaïre). Mémoire de licence inédit, Fac. Sci., UNIKIS, 48p.

Rahm, U. (1966). Les Mammifères e la forêt équatoriale de l'Est du Congo. *Ann. Mus. Roy. Afr. Cent., Tervuren,* Série 8, 149 : 38-121.

Rahm, U. (1970). Note sur la reproduction des Sciuridés et Muridés dans la forêt équatoriale du Congo. *Rev. Suisse de Zool.,* 77 : 635-646.

Ramade, F. (1984). Élément d'Écologie. Écologie Fondamentale. MacGraw-Hill, Paris, 404 p.

Sikubwabo, K. (1987). Contribution à l'étude de l'écoéthologie de l'Okapi (*Okapia johnstoni* Sclater, 1901) femelle dans la forêt de l'Ituri : rythme d'activités journalières, fréquentation du milieu, distances parcourues et domaine vital. Mémoire, Fac. Sci. UNIKIS, inédit, 50 p.

Tshombe, R. (1994). Census report of humain populations in and around the Réserve de Faune à Okapis. For Wildlife Conservation Society.

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Cytotaxonomy of rodent species from Ethiopia, Kenya, Tanzania and Zambia

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ABSTRACT. An extended survey of taxa belonging to two genera of Cricetomyinae (*Cricetomys* and *Saccostomus*), one Gerbillinae (*Gerbilliscus*), eight Murinae (*Acomys*, *Aethomys*, *Arvicanthis*, *Lemniscomys*, *Mus* (*Nannomys*), *Mastomys*, *Grammomys*, *Stenocephalemys*) and one Myoxidae (*Graphiurus*) was carried out as part of the EU programme "Staplerat" involving Ethiopia, Kenya, Tanzania and Zambia. Here we report the diploid and autosomal fundamental numbers of these rodent taxa. Seventeen of them were unknown, for four we report chromosomal variants and for another 16 new localities where they occur. We discuss their specific status taking into consideration our results together with data from literature and highlight the problems in taxonomy and systematics that are yet to be solved, due do their extended range and the occurrence of species complexes. We highlight cases for which there should be a re-evaluation of specific names that were not included in the last rodent checklist.

KEY WORDS : Cytogenetics, Rodents, taxonomy, East Africa.

INTRODUCTION

Current knowledge of African rodent taxonomy has been largely influenced by the history of colonization and by several expeditions organised independently by major museum Institutions carried out during the early part of the twentieth century. As a result, Natural History museums in Europe and in the United States posses the largest collections of African rodents, which include most species types so constituting a unique reference for correct taxonomic identification and classification purposes. It is worthy of note that, although essential from a scientific point of view, this resulted in a proliferation of names, as most descriptions were carried out with little or limited comparison to the large series, which is the only way to arrive at the correct identification of variation (e.g., the long list of taxa reported by ALLEN in 1939).

The second part of the twentieth century saw the development of new approaches, such as cytogenetics, genetics, molecular genetics and morphometrics which first separately and later combined into a multidisciplinary approach have been employed to study African rodent taxonomy, and often in collaboration with African Institutions. This approach was based on the biological species concept derived from the Modern Synthesis (DOBZHANSKY, 1937). However, most of this work was carried out on a local scale which has limited its full application. Much of the information on African Rodents is scattered over wide areas, and taxonomic revision for many of the genera is far from compete. This is also a consequence of the occurrence of sibling and cryptic species. Therefore, there is a need for continuing collaboration in order to allow investigations to cover larger areas.

The Staplerat project[1], founded by the European Union and involving Ethiopia, Kenya, Tanzania and Zambia as

* Walter Verheyen deceased late 2005 after acceptance of this paper. He was a great example for all other authors of this paper and for African rodent taxonomy in general.

[1] STAPLERAT, Protecting staple crops in eastern Africa: integrated approaches for ecologically based field rodent pest management. An international collaborative project, supported by the European Union's 5th Framework RTD Program.

African partners, constituted an excellent opportunity to investigate rodent taxonomy on a larger scale. The study concerned an area which extended from the Ethiopian plateau south to northern Zambia across the eastern side of the Great Rift Valley of Kenya and Tanzania. The programme involved the identification of integrated approaches for rodent pest control in agricultural areas. This naturally implied a need for a correct taxonomy of these captured species.

The areas studied formed two main biotic zones typical of the eastern part of Africa, i.e. the Somali-Maasai and the Zambezian (MENAUT, 1983; WHITE, 1986). These areas represent independent cradles of speciation and evolution for different rodent faunas, from the Late Miocene to the present day (DENYS, 1999). Our study reports the genera and species which, in addition to those in the dry and wet Miombo woodland savannas, provide evidence of this recent history.

The limit between the Somali-Maasai and the Zambezian biomes occurs in south western Tanzania and northwest Zambia (Fig. 1), and represents a crucial area where independently evolved rodent faunas converge. Furthermore, our sampling localities extend to the northwest of the Somali-Maasai, across the Pare and Uzambaras range dividing the Kenyan and Tanzanian savannas, up to the deciduous bushland and thicket which characterizes the bottom of the Rift which penetrates and bisects the Ethiopian plateaux.

During the three-year project there were several collections, both in fields and surrounding areas. Samples of each taxon found at each locality were studied using multidisciplinary approaches, including cytogenetics, molecular genetics and morphometrics. Here we present the cytotaxonomic results, providing the diploid (2n) and fundamental numbers (NFa) only. A description of each karyotype by means of differential staining will appear elsewhere for each genus as a separate paper.

Karyotype descriptions constitute the primary tool for rodent species identification, as it has been established and generally accepted that the reason behind the high diversity shown by this mammalian order is related to its high rate of chromosomal mutation (CORTI, 2002; KING, 1993). We present here the karyotypes for two genera of Cricetomyinae (*Cricetomys* and *Saccostomus*), one Gerbillinae (*Gerbilliscus*), eight Murinae [*Acomys, Aethomys, Arvicanthis, Lemniscomys, Mus (Nannomys), Mastomys, Grammomys, Stenocephalemys*] and one Myoxidae (*Graphiurus*).

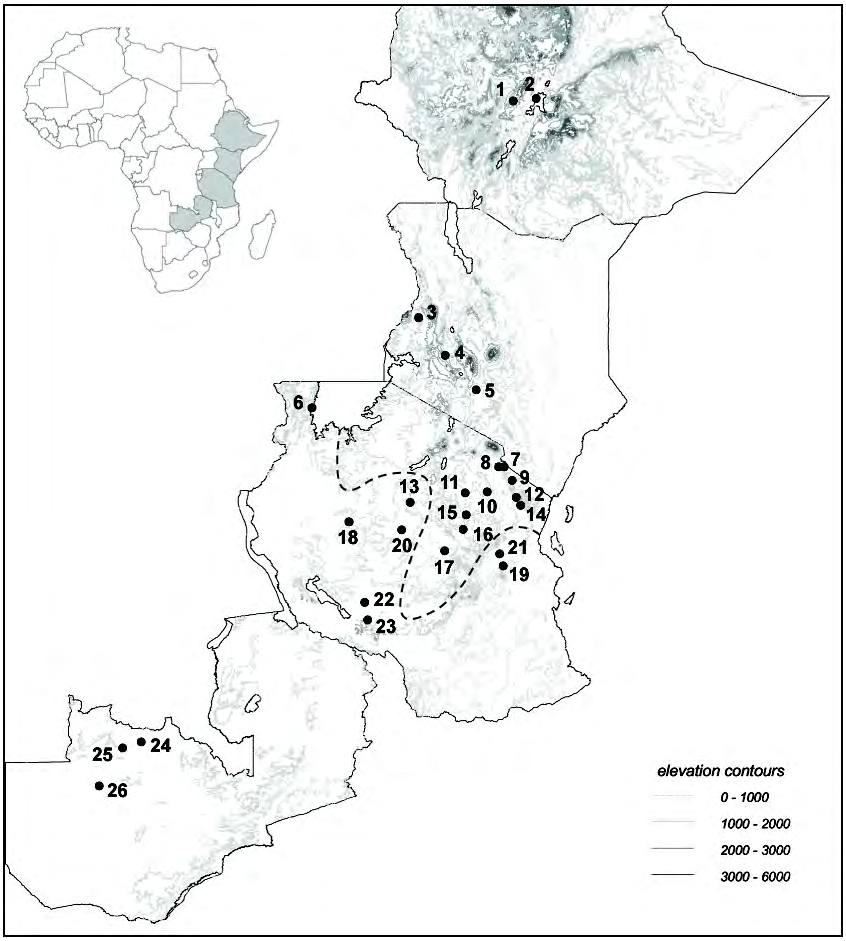

Fig. 1. – Map of Ethiopia, Kenya, Tanzania and Zambia (as indicated in the inset) with the collection localities (see Table 1 for the locality names and description). Elevation contour intervals are also shown. The dotted line represents the border between the Somali-Maasai (North) and the Zambezian (South) biotic zones.

MATERIAL AND METHODS

The following eight localities were sampled (STAPLERAT, 2003): Mugo and Zeway (Ethiopia); Rongai, Kitale and Nairobi (Kenya); Chunya (Tanzania); Meheba and Mutoma (Zambia) (Fig. 1; Table 1). These are prevalently arable fields (for the original habitat description, see Table 1). To achieve a more realistic representation of species range outside of the project areas, captures in surrounding localities were included, particularly in the geographic gaps between the field study areas (Fig. 1; Table 1).

Specimens were live-trapped using Sherman Folder traps and then transported alive to the following laboratories: Biology Department, Addis Ababa University (Ethiopia); Department of Zoology, Kenyatta University (Kenya); Pest Management Centre, Sokoine University of Agriculture, Morogoro (Tanzania); Mutanda Agricultural Research Station, Solwezi (Zambia).

Chromosome preparations were obtained from the bone marrow following the air-drying method of HSU & PATTON (1969). Cell suspensions in fixative were then transported to the Dipartimento di Biologia Animale e dell'Uomo, Università di Roma 'La Sapienza', where slides were prepared. Metaphases were stained by the Giemsa standard method (pH7). Pictures of metaphases were collected using the digital camera Photometrics Sensys 1600 and the Iplab software (Scanalytics, Inc, version 2.420).

Taxonomic definitions for Muroidea followed the most updated check-list by MUSSER & CARLETON (2005) and, for Myoxidae, HOLDEN (1993). Specimen identification was based on comparisons with type material and relevant series. We discuss the taxonomic problems encountered in species identification and description. For species whose taxon is in doubt, chromosomal comparisons and analysis of the sequences of mitochondrial genes were carried out in an integrated approach in order to make identification possible (such results will appear elsewhere). However, it was not possible to reach a definitive taxonomic definition for some. These are provisionally indicated in the following sections as "cf.", "cfr.", "sp.", or with an acronym.

A total number of 187 specimens representing 37 putative species were analysed. Specimens are preserved at the permanent collection of Musée Royal de l'Afrique Centrale, Tervuren (codes starting with a "T") and of the Museo di Anatomia Comparata dell'Università di Roma "La Sapienza" (codes with "ET", "ZM", "KE", "TZ").

TABLE 1

Collection localities, with the locality code for Fig. 1, latitude and longitude, and the current and original habitat (see, for habitat reference, White, 1983)

Country	Locality	Locality code	Latitude and Longitude	Habitat	Original habitat
Ethiopia	Mugo	1	07°50'N - 37°59'E	Enset fields	Highland with some alpine vegetation and moorland
	Zeway	2	07°55'N - 38°43'E	Maize fields	Savannah woodland with acacia trees
Kenya	Kitale	3	01°01'N - 35°00'E	Maize fields	Mosaic of lowland rainforest and secondary grassland
	Rongai	4	00°10'S - 35°51'E	Maize fields	Mosaic of East African evergreen bushland and secondary *Acacia* wooded grassland
	Nairobi	5	01°16'S - 36°49'E	Grassland around buildings	" "
Tanzania	Kitundu Forest	6	01°53'S - 31°39'E	Rain forest	Rain forest
	Jipe	7	03°41'S - 37°42'E	Savannah bushes with scattered trees	Savannah bushes with scattered trees
	Lwami	8	03°41'S - 37°32'E	Bushland with scattered trees	Bushland with scattered trees
	Kisiwani	9	04°07'S - 37°57'E	Scattered bushes and grassland	Scattered bushes and grassland
	Ngasumet	10	04°29'S - 37°10'E	Grassland with scattered bushes	Grassland with scattered bushes
	Matongolo	11	04°31'S - 36°28'E	Bushland	Bushland
	Mkomazi	12	04°39'S - 38°05'E	Wooded grassland	Wooded grassland
	Singida	13	04°49'S - 34°44'E	Wooded grassland	Wooded grassland
	Mombo	14	04°54'S - 38°13'E	Grassland with scattered bushes	Grassland with scattered bushes
	Ndaleta	15	05°12'S - 36°30'E	Grassland	Grassland
	Zoissa	16	05°40'S - 36°25'E	Bushland	Bushland
	Mvumi Mission	17	06°20'S - 35°50'E	Wooded grassland	Wooded grassland
	Inala	18	05°25'S - 32°49'E	Grassland with scattered bushes	Grassland with scattered bushes
	Morogoro	19	06°49'S - 37°40'E	Cultivated areas, with fallow, scattered trees	Wooded grassland
	Itigi	20	05°41'S - 34°28'E	Bushland	Bushland
	Dakawa	21	06°26'S - 37°34'E	Miombo woodland	Miombo woodland
	Chunya B	22	07°58'S - 33°18'E	Cultivated fields, grassland with scattered trees	Wetter Zambezian Miombo woodland
	Chunya A	23	08°31'S - 33°24'E	Wetter Zambezian Miombo woodland	" "
Zambia	Mutanda Res. Station	24	12°22'S - 26°16'E	Maize fields	" "
	Meheba	25	12°33'S - 25°41'E	Maize fields	" "
	Mutoma	26	13°45'S - 24°57'E	Maize fields	" "

Karyotype descriptions

CRITETOMYNAE (Roberts, 1951).

The subfamily Cricetomyinae comprises three genera, *Beamys* (Thomas, 1909) [with two species *B. hindei* (Thomas, 1909) and *B. major* (Dollman, 1914)], *Cricetomys* (Waterhouse, 1840) (with four species), and *Saccostomus* (Peters, 1846), [with the two species *S. campestris* (Peters, 1846) and *S. mearnsi* (Heller, 1910)].

– *Cricetomys* (Waterhouse, 1840).

There are currently four recognised species of giant pouched rats (GENEST-VILLARD, 1967): *Cricetomys ansorgei* (Thomas, 1904), *C. emini* (Wroughton, 1910), *C. gambianus* (Waterhouse, 1840), and *Cricetomys kivuensis* (Lönnberg, 1917). Previously it was suggested that there existed six (ALLEN, 1939) or one (ELLERMAN et al., 1953) species, while GENEST-VILLARD (1967) described predominantly savannah-dwelling (*C. gambianus*) and lowland forest (*C. emini*) species. There are limited data regarding possible variation, so taxonomy must be considered as provisional for East Africa. Chromosomal descriptions are available for West African specimens only. MATTHEY (1954) described a karyotype for *C. gambianus* (unknown origin) with 2n=78. In Senegal, GRANJON et al. (1992) found a karyotype with 2n=80 and NFa=82, and in Benin, CODJA et al. (1994) described a karyotype with 2n=82 and NFa=88 for *C. gambianus*, and a karyotype of 2n=80 and NFa=88 for *C. emini*.

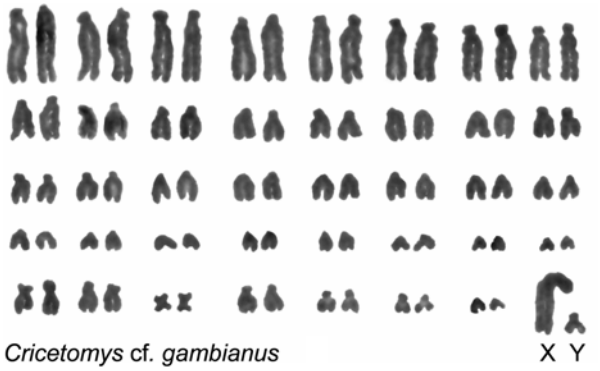

Fig. 2. – The karyotype of *Cricetomys* cf. *gambianus*, 2n=80 and NFa=84, X Y.

– *Cricetomys* cf. *gambianus* (Thomas, 1904).

One male from Morogoro (TZ), no voucher specimen. No morphological and DNA comparisons are possible for the moment. Therefore, we refer to this cytotype as "cf. *gambianus*". The diploid number is 2n=80 and the NFa=84. The autosomes are composed of seventy-four acrocentrics decreasing in size and by four medium and small metacentrics (Fig. 2). The X chromosome is one of the largest chromosomes of the whole karyotype and it is biarmed. The Y chromosome is a medium-size submetacentric. This karyotype differs from those in Senegal (GRANJON et al., 1992) and Benin (CODJA et al., 1994): not only are the diploid and NFa different, but also several pairs of acrocentrics are characterized by the occurrence of small arms, which do not occur in the other karyotypes. This karyotype is described here for the first time.

– *Saccostomus* (Peters, 1846).

Saccostomus is common and widespread in savannahs, scrubby areas, and cultivated fields from South Ethiopia and Somalia through East Africa down to the Cape Province. Despite this commonness, taxonomy has long been a source of debate (DELANY, 1975; ELLERMAN et al., 1953; MISONNE, 1974). In fact, the most recent rodent checklist (MUSSER & CARLETON, 2005) includes two species only, i.e. *S. campestris* (Peters, 1846) and *S. mearnsi* (Heller, 1910). However, a wide karyotypic polymorphism within the genus has been described, from the extreme south of the range (GORDON, 1986) to the north (CAPANNA et al., 1985; CORTI et al., 2004) through the central part of Africa (FADDA et al., 2001; HUBERT, 1978). Recently, a combined approach using both cytochrome *b* sequences groups and cytogenetics (CORTI et al., 2004) established that *mearnsi* and *campestris* represent two distinct natural groups and species complexes and was able to suggest a partial taxonomic resolution of the genus.

– *Saccostomus* cf. *elegans* (Thomas, 1897).

Three different karyotypes have been found. Two of them occur in two nearby localities (approximately 15 km apart) in south Tanzania, named Chunya A and B; a third is typical of northwest Zambia (Fig. 1, Tab. 1).

Tanzania, Chunya A (♀T50664). The diploid number is 2n=42 and the NFa is 46. The X chromosome is a medium-size submetacentric. The karyotype includes two pairs of large submetacentrics and two pairs of very small metacentrics, the remaining chromosomes being acrocentrics decreasing in size (see CORTI et al., 2004, for a Giemsa stained karyotype).

Tanzania, Chunya B 2 (♀TZ522, ♀TZ524, ♂TZ502, ♂TZ519, ♂TZ520). The diploid number is 2n=44 and NFa=46. The karyotype consists of three pairs of biarmed autosomes, one of which is a large subtelocentric and two are small metacentrics; the remaining autosomes are acrocentrics decreasing in size. The X and Y chromosomes are a large metacentric and a medium size submetacentric, respectively (see CORTI et al., 2004, for a Giemsa stained karyotype).

Zambia *Saccostomus* sp., Mutanda Research Station (♂ZM3, ♂ZM9, ♂ZM15, ♂ZM18). The diploid number is 2n=44 and the NFa is 48. The autosomal complement is identical to the one described for Chunya B, except for a pair of small metacentric chromosomes (No 20; in CORTI et al. 2004) that in Chunya B are acrocentrics. Furthermore, the X chromosome is a large submetacentric and Y is a medium size metacentric.

On the basis of the entire sequence of the cytochrome *b* mitochondrial gene, CORTI et al. (2004) have shown that these three karyotypic forms belong to the *campestris* species group and that they all form a monophyletic clade typical of the Zambezian domain, the northern limits of which occur in southern Tanzania. There is a low proportion of nucleotide substitutions between them, suggesting that the ongoing chromosomal differentiation has not led to full speciation. The southern Tanzanian specimens

(Chunya A and B) occur north (230 km) of Karonga, the locality on the northern shores of Lake Nyasa from which *S. elegans* (Thomas, 1897) was described. However, a craniological comparison of our specimens with the type of *S. elegans* (BMNH 97.18.1.207) and of two "co-types" of *S. campestris* (BMNH 7.1.1.181 and 58.6.18.19) revealed that the Chunya specimens could also be allocated to typical *campestris*, whereas the northern Zambian specimens closely resemble the *elegans* type skull. However, the skull differences between the two groups could also be due to age differences (indeed, the *elegans* type skull is of an old individual, and the "co-types" of *campestris* are young animals). It is obvious that this taxonomic problem will only be solved by undertaking an adequate study of 1) the sexual dimorphism and skull growth in a statistically relevant population of *Saccostomus* from the region concerned and of 2) the karyology and genetics of *Saccostomus* individuals from the Tette region in Mozambique (topotypical for *S. campestris*).

One must remember that a new undescribed species occurs in Tanzania north of the border with the Zambezian domain in the Maasai Steppe (FADDA et al., 2001). It has been shown (CORTI et al., 2004) that this new taxon belongs to the *Saccostomus* cf. *mearnsi* complex.

GERBILLINAE (Gray, 1825).

– *Gerbilliscus* (Thomas, 1897).

Gerbilliscus has been proposed recently as a distinct genus from *Tatera* (PAVLINOV, 1999; CHEVRET & DOBIGNY, 2005). It includes exclusively all the African species of the former *Tatera* (Lataste, 1882), an Asian monospecific with only *T. indica* (MUSSER & CARLETON, 2005). According to this checklist, the genus now includes 10 species. However, recent molecular data (COLANGELO et al., 2005; COLANGELO et al., submitted) suggest the occurrence of cryptic species which cannot be recognized through cytogenetics and/or morphometrics (i.e. *G. vicinus*). Moreover, there is molecular (CHEVRET & DOBIGNY, 2005; COLANGELO et al., sub.) and cytogenetic evidence indicating a close relationship between *Gerbilliscus* and *Gerbillurus*. An extensive systematic revision would probably indicate *Gerbillurus* as synonymous of *Gerbilliscus* (CHEVRET & DOBIGNY, 2005; COLANGELO et al., sub.).

There have been a high number of karyotypic studies performed on the genus, but they all originate from scattered areas, and no serious attempt has been made to summarize and include them in a general framework. Data available for the African species are as follows: *G. afra* (2n=44, NFa=66; MATTHEY, 1954; QUMSIYEH, 1986), a South African endemic. *G. brantsii* (2n=44, NFa=66; MATTHEY, 1954; QUMSIYEH, 1986), ranging from South Africa to Zambia. *G. leucogaster* (2n=40, NFa=66; GORDON & RAUTENBACH, 1980; QUMSIYEH, 1986), ranging from South Africa to Southwest Tanzania; MATTHEY (1954) identified a specimen from the Central African Republic as *G. schinzi* but this species is now considered synonymous of *G. leucogaster*. *G. nigricaudus* (2n=36, NFa=68, COLANGELO et al., 2005), occurring in Kenya and Tanzania. QUMSIYEH et al. (1987) reported a karyotype with 2n=40 from Kenya (one specimen) which was attributed to *G. nigricaudus*. However, there is evidence that this karyotype would be better attributed to another species (COLANGELO et al., 2005). *G. robustus* (2n=36, NFa=64; QUMSIYEH et al., 1987; FADDA et al., 2001), but this should be attributed to *G. vicinus* (DOBIGNY et al., 2002; GRANJON & DOBIGNY, 2003; see later), occurring from Chad to the Horn and East Africa; two specimens from Central African Republic with 2n=46 and NFa=64 were identified by MATTHEY & PETTER (1970) as *G. robustus*, but this was probably incorrect, as later they were ascribed by QUMSIYEH et al. (1987) to *G. phillipsi* (Somalia, Kenya, and Ethiopia); MATTHEY & PETTER (1970) described a karyotype with 2n=36 and NFa=62 from a Central African Republic specimen and attributed it to *G. kempi,* but this would be better referred to as *G. robustus*. *G. kempi* (2n=48, NFa=62-64; CODJA et al., 1994; COLANGELO et al., 2001); GAUTUN et al. (1986) referred to a specimen from Guinea with 2n=46 as *G. kempi*. Samples with 2n=48-50 and NFa=52-66, attributed to *G. nigrita* (now included in *G. kempi*), were reported from Chad, Zaire, Zambia and Angola. MATTHEY & PETTER (1970) attributed specimens from Burkina Faso and Ivory Coast to *G. hopkinsoni* (2n=48, NFa=62-64), now synonymous of *G. kempi*. *G. gambianus* (synonymous of *G. kempi*) (2n=52, HUBERT et al., 1973); MATTHEY (1969) described in a specimen from Senegal 2n=52 and NFa=64 and this was ascribed to *G. validus*, but probably it should be considered *G. gambianus* (MATTHEY & PETTER, 1970). DOBIGNY et al. (2002) reported the same karyotype from Nigeria. *G. guineae* (2n=50, NFa=64; MATTHEY & PETTER, 1970; BENAZZOU et al., 1984; GAUTUN et al., 1985). More recently, BULATOVA et al. (2002) reported a karyotype from Ethiopia with 2n=52 and NFa=62 that was attributed to *G. validus*.

Two different karyotypes were found in the present study. One shows 2n=36 and NFa=68, which is shared by three different species distinguishable on the basis of skull morphology and molecular analyses (COLANGELO et al., 2005), i.e. *G. nigricaudus*, *G. robustus* and *G. vicinus* (for a discussion of their systematic status see COLANGELO et al., 2005). The second karyotype shows 2n=40 and NFa=66 and characterizes *G. leucogaster*.

– *Gerbilliscus leucogaster* (Peters, 1852).

Dakawa (♂T50545, ♂T50546); Tanzania. The diploid number is 2n=40 and NFa=66. The karyotype is composed of fourteen pairs of biarmed chromosomes decreasing in size and five pairs of medium size acrocentrics. The X chromosome is a large metacentric, and the Y is a medium size submetacentric (see COLANGELO et al., 2005). Phylogenetic analyses based on the cytochrome *b* and 16S mitochondrial genes showed a marked divergence between these specimens and those attributed to the *robustus* species group (i.e. *G. robustus*, *G. nigricaudus and G. vicinus* (COLANGELO et al., 2005).

– *Gerbilliscus robustus* (Cretzscmar, 1826).

Zeway (♂ET107, ♂ET119, ♂ET127); Ethiopia. The diploid number is 2n=36 and NFa=68. All autosomes are biarmed decreasing in size. The X chromosome is a large metacentric, and the Y chromosome is a small acrocentric (see COLANGELO et al., 2005). This same chromosomal

formula has already been reported from several other localities from west Africa along the arid sub-Saharan belt to East Africa down to Tanzania across the arid savannahs (QUMSIYEH et al., 1987; FADDA et al., 2001), suggesting that this karyotype is highly represented in this biome.

– *Gerbilliscus nigricaudus* (Peters, 1878).

Mkomazi (♀T50216, ♀T50217), Lwami T50230, Jipe (♀T50453, ♀T50475, ♀T50476, T50456♂); Tanzania. The diploid number is 2n=36 and NFa=68. All autosomes are biarmed decreasing in size. The X chromosome is a large metacentric, and the Y chromosome is a small acrocentric (see COLANGELO et al., 2005). We found this species in a restricted area across the border of Tanzania and Kenya. MATTHEY (1969) and QUMSIYEH et al. (1987) reported for *G. nigricaudus* a diploid number of 40 with NFa respectively 66 and 68, but probably these specimens are referable to *G. leucogaster*.

– *Gerbilliscus vicinus* (Peters, 1878).

Itigi (♀T50339), Matongolo (♂T50062), Ndaleta (♂T50144, ♀T50153, ♀T50158), Inala (♂T50579), Ngasumet (♂T50190), Mombo (♀T50214, ♀T50215, ♀T50226, ♂T50227), Jipe (♀T50473); Tanzania. Nairobi (♀KE135); Kenya. The karyotype appears to be the same as *G. robustus* from Ethiopia, but these samples show a marked genetic divergence from the Ethiopian specimens suggesting that *G. vicinus* should be considered a separate species (COLANGELO et al., 2005). BATES (1988) reported a significant geographical variation in skull and body size in *G. robustus*, suggesting the possible occurrence of a distinct race in central Tanzania. He identified *G. swaythlingi* (Kershaw, 1921), type locality Morogoro, as the holotype for this race. However, an extensive morphometric and molecular genetic comparison would probably ascribe this race to *G. vicinus*.

MURINAE (Illiger, 1815).

– *Acomys* I. (Geoffroy, 1838).

These spiny mice are widespread throughout all of Africa, the near and Middle East, and some Mediterranean islands. The rodent checklist by MUSSER & CARLETON (2005) lists 19 species, but as for most of the other African rodent genera, their taxonomy and systematics are yet to be established. Cytogenetics, morphology and, recently, molecular genetics (BAROME et al., 1998; 2001) have been widely used to shed some light on the taxonomy and systematics of the genus.

Since the first descriptions of the karyotype of *Acomys* by MATTHEY (1956; 1963; 1965a, b; 1968), further data concerning chromosomal variation in the genus have been added by several authors. Originally there was considerable interest in the karyotype of *A. selousi*, long considered synonymous of *A. spinosissimus* (see MUSSER & CARLETON, 1993). The peculiar chromosomal sex determination found in the former, with a single and exceptionally large X chromosome in both males and females, was in striking contrast with the XX/XY typical of *A. spinosissimus* and the other species of the genus. Furthermore, MATTHEY (1965a, b, and unpublished) also showed an inter- and intra-individual variability in chromosome constitution in *A. selousi*. Later, DIPPENAAR & RAUTENBACH (1986) found the same 2n=60 and NFa=68, but with a submetacentric X in Transvaal (South Africa). All together, these data do not support the idea of maintaining the two taxa in synonymy, and they should be definitively considered as separate valid species.

The analysis of a partial fragment (715 bp) of the gene for cytochrome *b* in the Tanzanian samples, for which we report here the karyotypes (unpublished data), confirmed that *A. spinosissimus* and *A.* cf. *selousi*, although monophyletic, constitute two well separated species. This genetic and chromosomal distinction is also reported for the Tanzanian locality of Berega by BAROME et al. (2001). For these reasons, we decided to provisionally maintain the name *A.* cf. *selousi* for these specimens until the "*selousi*" – like group has received adequate investigation. The karyotypes known for other species are as follows: *A. cahirinus*, 2n=36 and NF=68 (VOLOBOUEV et al., 1996); *A. dimidiatus* (cf. *A. airensis*, Agades, Niger, 2n=42, NFa=66), 2n=38 and FN=70 (VOLOBOUEV et al., 1991); *A. ignitus*, 2n=50 and NF=66-68 (MATTHEY, 1956); *A. russatus*, 2n=66 and NF=66 (WAHRMAN & ZAHAVI, 1953).

Following the 1999 expedition in the Maasai Steppe, FADDA et al. (2001) reported three different karyotypes for this part of Tanzania, corresponding to *A. spinosissimus* (2n=60, NFa=70), *A. wilsoni* (2n=62, NFa=76) and *A. ignitus* (2n=36, NFa=68). Here we add further information from a higher number of localities and for a higher number of specimens for these species.

– *Acomys spinosissimus* (Peters, 1852).

Chunya (♀T50676, ♀T50673), Tabora-Inala (♀T50676), Zoissa (♀T50119, ♀T50088, ♂T50087, ♂T50202), Matongolo (♀T50003); Tanzania. The species occurs in a typical Zambezian domain (Southern Tanzania to Southern Transvaal). However, it extends north to the Maasai Steppe, which is a typical Somali-Maasai arid domain. The diploid number in the localities investigated is 2n=60 and the NFa=70. The karyotype is represented by 5 pairs of metacentrics and submetacentrics, 22 pairs of acrocentrics decreasing in size, and one pair of small metacentrics. The X chromosome is a large acrocentric and the Y-chromosome is a small subtelocentric. This karyotype is the same as the one described by FADDA et al. (2001) in the Maasai Steppe and by DIPPENAAR & RAUTENBACH (1986) in South Africa.

– *Acomys* cf. *selousi* (Roberts, 1951).

Dakawa (♀TZ521); Tanzania. The diploid number is 2n=59, NFa=68. The karyotype is constituted by five pairs of medium size biarmed chromosomes, 24 pairs of acrocentrics decreasing in size (Fig. 3). The single X chromosome is very large.

Fig. 3. – The karyotype of *Acomys* cf. *selousi*, 2n=59 and NFa=68. Note the single X chromosome of very large size.

– *Acomys wilsoni* (Thomas, 1892).

Jipe (♀T50467, ♂T50463, ♀T50466, ♂T50439, ♀T50440, ♀T50447, ♀T50446, ♀T50438, ♂T50437), Ngasumet (♂T50246, ♂T50247, ♀T50247); Tanzania. The range of the species includes Sudan, Ethiopia, Somalia, Kenya and Tanzania, but its limits are unknown. The first description of the karyotype of the species was first described by FADDA et al. (2001). The diploid number is 2n=62 and NFa=76. The autosomal set is composed of eight pairs of meta- and submetacentric chromosomes, three of which are the largest of the set and five of which range from medium to small, and of 22 pairs of acrocentrics decreasing in size. The X chromosome is acrocentric (the largest amongst the acrocentrics) and the Y chromosome is a small acrocentric.

– *Acomys ignitus* (Dollman, 1910).

Lwami (♂T50232, ♂T50527, ♀T50529, ♂T50528, ♂T50517, ♂T50499, ♂T50505), Ngasumet (♀T50185); Tanzania. The range includes Tanzania and Kenya, but its limits are unknown. Samples were collected at the extreme North of the Maasai Steppe, where a corridor with Southern Kenya is present through the Uzambaras and the Pare mountain range. The first description of the karyotype was given by FADDA et al. (2001) and shows 2n = 36 and NFa = 68. The karyotype resembles *A. cahirinus* and, in fact, the species was included by ELLERMAN (1941) in the *Cahirinus* group.

– *Aethomys* (Thomas, 1915).

The genus has traditionally been divided into two subgenera (DAVIS, 1975): *Micaelamys*, including *A. namaquensis* and *A. granti*, and *Aethomys*, for which nine species are currently recognised (MUSSER & CARLETON, 2005; VISSER & ROBINSON, 1986). Following the original hypothesis by DAVIS (1975), the two subgenera can be distinguished on the basis of tail length and colour of ventral parts.

Chromosomal studies (MATTHEY, 1954; VISSER & ROBINSON, 1986; BAKER et al., 1988) have shown that the karyotypes of the "*Micaelamys*" *A. namaquensis* (2n=24) (from Southeast Zambia to South Africa) and *A. granti* (2n=32) (Cape Province) are divergent from the other species studied, which are all characterized by higher diploid numbers (2n=44-50). Recent molecular analyses based on cytochrome *b* sequences (DUCROZ et al., 2001; RUSSO et al., 2001; CASTIGLIA et al., 2003a) confirmed the high genetic difference between the two subgenera and provided evidence for the paraphyly of the genus in a wider phylogenetic context involving several other African species of Murinae and Otomynae (DUCROZ et al., 2001; CASTIGLIA et al., 2003a). These data suggest the need for a definitive splitting of the genus.

There is also evidence indicating the occurrence of cryptic species. For example, it has been recognised that *A. chrysophilus,* widespread from Kenya to South Africa, must be separated into two species, corresponding to different cytotypes previously identified (GORDON & RAUTENBACH, 1980; GORDON & WATSON, 1986; VISSER & ROBINSON, 1986): the true *A. chrysophilus* (2n=50) and *A. ineptus* (2n=44). These two species occur sympatrically and differ in gross sperm and bacular morphology (VISSER & ROBINSON, 1986; BREED et al., 1988) as well as in their quantitative cranial traits (CHIMIMBA, 1998; CHIMIMBA et al., 1999).

– *Aethomys kaiseri* (Noack, 1887).

Meheba, Solwezi (♂ZM13, ♂ZM32); Zambia. The diploid number is 2n=50 and NFa=60. The karyotype is composed of forty-five pairs of acrocentric chromosomes decreasing in size and five pairs of small meta/submetacentrics. The sex chromosomes are very large and biarmed with the Y being slightly larger that the X chromosome. The length of each sex chromosome is approximately double the length of autosome pair 1. The karyotype is reported in CASTIGLIA et al. (2003a).

– *Arvicanthis* (Lesson**,** 1842).

Arvicanthis probably represents one of the African rodent genera that has received most attention over the last decade. As a result, the number of species recognised increased to seven after the latest rodent checklist (MUSSER & CARLETON, 2006). Previously, CORBET & HILL (1991) and MUSSER & CARLETON (1993) recognized five species only (although with some disagreement regarding their systematics and taxonomy). The numerous studies performed on a chromosomal (BASKEVICH & LAVRENCHENKO, 2000; CAPANNA & CIVITELLI, 1988; CAPANNA et al., 1996; CASTIGLIA et al., 2003b, 2006; CIVITELLI et al., 1995; FADDA et al., 2001; VOLOBOUEV et al., 1987; 1988; 2002a; GRANJON et al., 1992), allozymic (CAPULA et al., 1997), mtDNA sequencing (DUCROZ et al, 1997; CORTI et al., submitted), and morphometric (AFEWORK BEKELE et al., 1993; CORTI & FADDA, 1996; FADDA & CORTI, 1998; 2001) basis have shown that the genus is represented by a higher number of species.

Two major clades occur within *Arvicanthis*, roughly an eastern and a western one, although some of the western species extend into the East and vice versa (DUCROZ et al., 1997; CORTI et al., submitted). This result is based on molecular studies (and congruent with karyotypic analyses). Taxonomic confusion in the past, part of which remains unsolved, is probably due to the high level of convergence shown in morphology, which obscures species differences (FADDA & CORTI, 2001).

The karyotypes of the taxa recognized so far are as follows: *A.* cf. *somalicus*, 2n=62, NFa=62-63 (Ethiopia; Baskevich & Lavrenchenko, 2000). *A. abyssinicus*, 2n=62, NFa=62 (Ethiopia; Corti et al., 1996). *A. blicki*, 2n=48, NFa =64 (Ethiopia; Corti et al., 1995; 1996). *A. neumanni,* 2n=54, NFa=62 (Tanzania; Fadda et al., 2001; Castiglia et al., 2003b). *A. nairobae,* 2n=62 NFa=78 (Tanzania; Fadda et al., 2001; Castiglia et al., 2003b). *A. ansorgei*, 2n=62, NFa=74/76 (Senegal, Mali, Burkina-Faso; previously named ANI-3; Volobouev et al., 2002a). *A. rufinus* (Benin; previously named ANI-4; Civitelli et al., 1995; Volobouev et al., 2002a). "*A. niloticus"* complex, 2n=62, NFa=62/64, described from Egypt, Sudan, Ethiopia, northern Senegal and northern Burkina Faso, southern Mauritania, Mali, Niger, Chad; Volobouev et al., 1988; 2002a; Philippi, 1994; Ducroz et al., 1997; Civitelli et al., 1995).

There are further karyotypes described for which there is still no species assignment or evidence supporting the original allocation made by authors. This is the case for the karyotype with 2n=44 and FN=72 described in Somalia by Capanna & Civitelli (1988), which was attributed to *A. niloticus,* which evidently characterizes a different unidentified species. In their recent review, Castiglia et al. (2006) defined this taxon with the acronym ANI-8. Furthermore, the situation is particularly confusing in Ethiopia, where a karyotype with 2n=60 and NFa=76 has been described in Konso (Gamo-Gofa, South Ethiopia; Orlov et al., 1992) and another one with 2n=56 and NFa=78 in Gambella (Bulatova et al., 2002).

The karyotypic results following the field studies of the Staplerat project are presented here for *A. nairobae* and for a number of taxa for which there is yet to be any definitive taxonomic solution. The latter highlight a complex pattern of sibling species and speciating taxa. This is particularly true for the *A. niloticus* complex that will be discussed first. Two other unknown karyotypes are indicated as ANI-5 and ANI-6.

– *Arvicanthis niloticus* (Desmarest, 1822 complex).

The two taxa *A. niloticus* and *A. dembeensis* (Rüppel, 1842) have been considered either as synonymous (see Musser & Carleton, 1993) or as separate species (see Yalden et al., 1976). *A. niloticus* (type localities: Upper Egypt, Fayum and Giza areas, part of the Nile delta), surprisingly, has received limited attention in all studies. Fadda & Corti (1998) examined, through three dimensional geometric morphometrics, the geographic variation in *A. niloticus* along the Nile Valley from Cairo down to the extreme south of Sudan, also including *A. testicularis* (Dollman, 1911) (synonymous of *A. niloticus*; Musser & Carleton, 2005). They evidenced in *A. niloticus* a north-south clinal variation in morphometric traits which somehow contrasts in direction that characterizing *A. testicularis*. This was considered by the Authors as sufficient to keep them as separate taxa, but the problem should be better addressed through a cytogenetic and molecular approach. Moreover, also the karyotype and the DNA analyses on *A. niloticus* were from samples of breeding colonies outside the topotypical area. *A. dembeensis* has been described as endemic to Ethiopia, and is considered a relatively 'lowland' taxon, occurring from sea level to 2000 mt a.s.l. (Yalden et al., 1976). However, there are problems regarding the taxonomic status of the samples so far analysed in different studies. The first one concerns the type specimen. To date, the most complete study was carried out through multivariate morphometrics (Afework Bekele et al., 1993) on eight localities (four of them from the bottom of the Rift along the Ethiopian lakes), which confirmed a clear morphological distinction from the other major taxon occurring in the country, i.e. *A. abyssinicus*. One of the populations examined was from Lake Tana, on the western side of the Rift Valley, i.e. the topotypical area from which Rüppel described the type specimen in 1842 (Deraske, 12° 25' N - 37° 20' E). This population clustered with the others that occurred on the eastern side of the Rift at altitudes below 2000 mt a.s.l. This morphological relatedness was considered sufficient to include them all under *A. dembeensis*. On this morphological basis, Corti et al. (1995) attributed the karyotype of specimens from Koka to *A. dembeensis*, and so far this has been considered the typical karyotype of this species. However, the species was included by Musser & Carleton (2005) in *A. niloticus*. The comparison of the cytochrome *b* sequences of samples of *A. dembeensis* and *A. niloticus* from Egypt (although from a breeding colony, but with very low genetic differences from Ethiopian samples) (Ducroz et al., 1998; Corti et al., submitted) and the fact that the two share the same karyotype (Corti et al., 1996) do not support a specific distinction so that its synonymy with *A. niloticus* should be definitively accepted. On the other hand, due to the variability characterizing this complex, Corti et al. (submitted) still suggest this taxon should be referred to as *A.* cf. *niloticus* 1.

Zeway (♂ET110, ♂ET114, ♂ET125, ♂ET126, ♂ET127); Ethiopia. Kitale (♂KE119); Kenya. The diploid number is 2n=62 and the NFa is 62. The autosomal set is characterized by 58 acrocentrics decreasing in size and a pair of small metacentrics. The X chromosome is a large submetacentric (the largest chromosome in the set) and the Y chromosome is a metacentric of medium size. Although these Ethiopian and Kenyan specimens seem to all have the same karyotype, they show a genetic differentiation in progress (Corti et al., submitted). Therefore, these authors referred to the specimen from Kenya as *A.* cf. *niloticus* 5 and to those from Ethiopia as *A.* cf. *niloticus 2.* Furthermore, this karyotype is identical to the one described for *A.* cf. *niloticus* 1 (Koka, Ethiopia) by Corti et al. (1996) and for *A. somalicus* (Awash National Park, Ethiopia) by Baskevich & Lavrenchenko (2000).

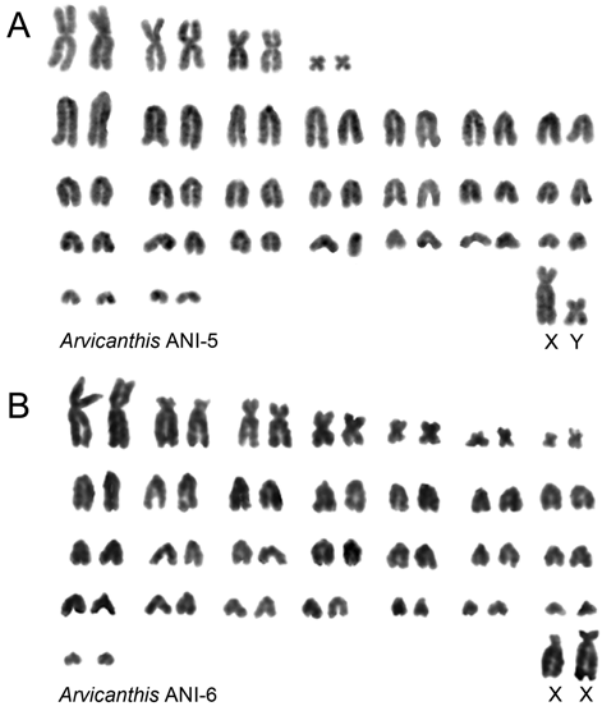

Fig. 4. – A) The karyotype of *Arvicanthis* ANI-5, 2n=56, NFa=62, X Y. B) The karyotype of *Arvicanthis* ANI-6, 2n=60, NFa=72, X X.

Arvicanthis sp ANI-5. Rongai (♂KE100, ♂KE103, ♂KE133, ♀KE127, ♀KE147); Kenya. The diploid number is 2n=56 and the NFa is 62. The autosomes are composed by three pairs of large metacentrics, one pair of small metacentrics, and 23 pairs of acrocentrics decreasing in size (Fig. 4A). The X chromosome is a large submetacentric and the Y chromosome is a medium size metacentric. This karyotype is described here for the first time. A banding study to assess the karyotype relationships with the other *Arvicanthis* in east Africa will appear elsewhere (Castiglia et al., 2005). A phylogenetic tree based on the entire sequence of the cytochrome *b* gene (Corti et al., submitted) suggests that this species is a member of the A. *niloticus sensu lato* group.

Arvicanthis sp ANI-6. Zeway (♀ET129); Ethiopia. The diploid number is 60 and the NFa is 72. The karyotype is composed by four pairs of large metacentric chromosomes, three pairs of small-sized metacentrics, and 22 pairs of acrocentrics decreasing in size (Fig. 4B). The X chromosome is a large submetacentric (Fig. 4B). This karyotype is described here for the first time. A banding study to assess the karyotype relationships with the other *Arvicanthis* in east Africa will appear in print elsewhere (Castiglia et al., 2005). Orlov et al. (1992) found a karyotype in Konso (Gamo-Gofa region, South of Zeway, along the Rift Valley) which is very similar to this one, with the exception of two additional pairs of small metacentrics. It is still questionable whether all these South Ethiopian cytotypes represent a chromosomally polytypic species. A phylogenetic tree based on the entire sequence of the cytochrome *b* gene (Corti et al., submitted) has shown that the Zeway karyotype constitutes the sister group of *A. ansorgei* and belongs to the West African clade of *Arvicanthis*, which extends along the south Ethiopian Rift Valley at lower altitudes. Furthermore, karyotypic variants have been found in the Konso (2n = 60 and NFa = 76) and in the Gambella (2n = 56 and NFa = 78) regions by Baskevich & Lavrenchenko (2000), all resembling morphologically *A. niloticus*. It should be noted that these areas are more than 5° latitude south of the type locality, so that it is questionable whether these results highlight a chromosomally polytypic or different species. Baskevich & Lavrenchenko (2000) provisionally named the specimens from Konso and Gambella *Arvicanthis sp.*1 and *Arvicanthis sp.* 2, respectively. Fadda & Corti (2001) morphometrically examined the specimens from Konso, Gambella, and Omo (plus a Somalian population) and found that they share unique morphometric characteristics, so that they were provisionally named *A. sp.* 3.

– *Arvicanthis nairobae* (Allen, 1909).

Nairobi, type locality (♂KE145); Kenya. The karyotype is characterized by 2n=62 and NFa=78. The autosomal set is composed of 9 pairs of biarmed autosomes and 21 pairs of acrocentric chromosomes decreasing in size. The biarmed chromosomes are represented by two large submetacentrics, four pairs of medium size submetacentrics and three pairs of small metacentrics. The X and Y chromosomes are subtelocentric, of large and small size respectively. This karyotype is identical to the one described in Tanzania (Fadda et al., 2001; Castiglia et al., 2003b).

– *Lemniscomys* (Trouessart, 1881)

The striped grass mice genus *Lemniscomys* is widely distributed throughout the African sub-Saharan savannahs and in Northwest Africa. The taxonomy and systematics of the genus is complex as it includes twelve recognised species (Musser & Carleton, 2005) which are probably at different levels of morphological differentiation (Ellerman, 1941; Van der Straeten & Verheyen, 1980) and are included in different groups. These are the "*barbarus*" group (striped species), including *L. barbarus*, and *L. hoogstrali*; the *striatus* group (spotted species), including *L. bellieri*, *L. macculus*, *L. mittendorfi* and *L. striatus*; the *rosalia* group (plain coloured species), which includes *L. griselda*, *L. rosalia*, *L. linulus*, and *L. roseveari.* Van der Straeten & Verheyen (1980) found morphometric differences within the "s*triatus*" group, with *L. striatus* being similar to *L. linulus* (*Rosalia* group) and well differentiated with respect to *L. bellieri* and *L. macculus*, which instead clusters with *L. barbarus*. On the basis of multivariate morphometrics of skull linear measurements, Carleton & Van der Straeten (1997) recently split *L. barbarus* into two species, i.e. *L. barbarus* restricted to scrub vegetation along a narrow coastal strip in Morocco, Algeria and Tunisia, and *L. zebra* with a sub-Saharan distribution. Relationships between species still remain unresolved, except for the close relationship between *L. bellieri* and *L. macculus* (Ducroz et al., 2001).

There is a conspicuous number of karyotypic data showing the occurrence of several different diploid and fundamental numbers. Considerable chromosomal variation has been shown in West and Central Africa for *L.*

striatus by Van der Straeten & Verheyen (1985; Burkina Faso; 2n=44, NFa= 58), Gautun et al. (1985; Burkina Faso; 2n=43), Matthey (1959; Congo; 2n=48, NFa= ~56), Capanna et al. (1997; Benin; 2n=44; NFa=72-74), Castiglia et al. (2002b; 2n=44, NFa=68), Ducroz (1998) and Van der Straeten & Verheyen (1978) (Ivory Coast; 2n=44, NFa=58). The large differences in NFa in these specimens may be due, in part, to different interpretations of small heterochromatic chromosomal arms. *L. bellieri* seems to be characterized by a constant 2n=56 and NFa=60 karyotype in Burkina Faso and Ivory Coast (Van der Straeten & Verheyen, 1978; Ducroz, 1998; Tranier & Gautun, 1979). *L. barbarus* also seems to have the same constant karyotype across Morocco (Stitou et al., 1997; 2n=54, NFa=58), Ivory Coast (Matthey, 1954; 2n=54) and the Algerian Coast (Filippucci et al., 1986; 2n=54, NFa =58). *L. macculus* has been studied in Central African Republic (Ducroz, 1998; 2n=56, NFa=62) and *L. mittendorfi* in Cameroon (Fülling, 1992; 2n=56). Recent findings in Tanzania (Castiglia et al, 2002b; Fadda et al., 2001) have shown a karyotype with 2n=54, NFa=68 for *L. zebra*, and 2n=54, NFa=62 for *L. rosalia*. The latter presents striking differences with the 2n=48, NFa =62 form described by Ducroz et al. (1999) for *L. rosalia* in Kwazulu Natal. The two differ due to several rearrangements and, on this basis, Castiglia et al. (2002b) argued that the two taxa should be considered as separate species. The type locality of *L. rosalia* is Monda, Nguru Mtns., Tanzania and, therefore, the name should be kept for the Tanzanian specimens, and it was suggested that *L. calidior* (Thomas and Wroughton, 1908) should be used as the oldest available name for the South African taxon.

Furthermore, Castiglia et al. (2002b) maintained that species relationships based on karyotypes contrast with the views that consider the plain coloured species as primitive and the multi-striped ones as derived. *L. bellieri*, *L. macculus* and *L. zebra* have an ancestral karyotype and are characterised by a multi-striped or spotted pelage, while *L. rosalia* has a derived karyotype and is a plain coloured species. This hypothesis is also in agreement with the morphometric relationships outlined by Van der Straeten & Verheyen (1980), who found a strict morphological similarity between *L. barbarus* and *L. bellieri* /*L. macculus*.

Here we present the karyotype of *L.* cf. *striatus massaicus* from Kenya and additional material for *L. rosalia* and *L.* cf. *zebra* from Tanzania (these two occur sympatrically in several of the localities studied).

– *Lemniscomys rosalia* (Thomas, 1904).

Zoissa (♂50083), Jipe (♂T50458, ♂T50460, ♂T50461, ♂T50462, ♂T50479, ♀T50442, ♀T50459, ♀T50477, ♀T50478), Kisiwani (♀T50428, T50427, ♂T50391, T50429), Mbugani-Chunya (T0672), Morogoro (T50201, ♂T50208, ♂T50547, ♀T50490, ♀T50491, ♀T50548), Ngasumet (♂T50172, ♂T50186), Dakawa (T50551, T50552); Tanzania. The species is characterised by 2n=54 and NFa=62. The autosomes comprise three pairs of large subtelocentrics, two pairs of small metacentrics and twenty-one pairs of acrocentrics decreasing in size. The X chromosome is a submetacentric and the Y is a medium size submetacentric, with a polymorphism occurring in the former (Castiglia et al., 2002b). This karyotype has already been reported and described by Fadda et al. (2001) for other localities from the Maasai steppe.

– *Lemniscomys* cf. *zebra* (Heuglin, 1864).

Matongolo (♂T50030), Mvumi Mission (♀T50333), Ngasumet (♀50179, ♀T50178, ♂T50174), Kisiwani (♀T50429), Mbugani-Chunya (♀T50699), Itigi (♀T50348), Lwami (♂T50492, ♂T50518, ♂T50524, ♂T50525, ♀T50502, ♀T50523, ♀T50526, ♀T50507, ♀T50501) Ndaleta (♀T50152); Tanzania. The 2n is 54, and the NFa is 58. Autosomes are represented by one pair of large submetacentrics (the largest of the autosomal set), by two pairs of very small metacentrics and by acrocentrics decreasing in size. The X chromosome occurs in two forms, both submetacentric, differing in the length of the short arm. Castiglia et al. (2002b) studied the occurrence of the two forms and found similar frequencies. The Y chromosome is a medium size metacentric. This karyotype has already been reported and described by Fadda et al. (2001) for other localities from the Maasai steppe.

– *Lemniscomys* cf. *striatus massaicus* (Pagenstecher, 1885).

Rongai (♂KE105, ♀KE116), Nairobi (♂KE110, ♂KE112, ♀KE125, ♀KE137, ♀KE146); Kenya. These specimens are characterised by 2n=48 and NFa=54. The karyotype is composed of four pairs of meta-submetacentrics, the remaining autosomes being acrocentrics decreasing in size (Fig. 5). The chromosome X is a large submetacentric, the Y is a small metacentric. This karyotype is presented here for the first time. The chromosomal differences between these specimens and *L. striatus* from West Africa are significant. A description of chromosomal differences based on differential staining will be described elsewhere.

Fig. 5. – The karyotype of *Lemniscomys* cf. *striatus massaicus*, 2n=48, NFa=54, X Y.

– *Mus* (L., 1758), subgenus *Nannomys (*Peters, 1876).

The African species of the subgenus *Nannomys*, known also as *Leggada*, constitute one of the major taxonomic puzzles and an emblematic group due to their fast rate of speciation often associated with chromosomal rearrangements. They form a monophyletic group, the ancestor of

which migrated from Asia through Iraq, Iran, and Saudi Arabia into Ethiopia (JOTTERAND, 1972). CORBET (1990) has highlighted that although there can be no doubt regarding the dichotomy between *Nannomys* and *Mus sensu strictu*, the recognition of the former as a separate genus is still far from being solved. MUSSER & CARLETON (2005) listed 19 species in the subgenus, but this number is likely to increase due to the occurrence of cryptic and chromosomal species (VEYRUNES et al., 2004). Furthermore, VEYRUNES et al. (2005) recognised seven clades on the basis of cytochrome *b* sequences, probably corresponding to more species since some of these may correspond to species complexes.

Previous cytogenetic studies divided the species into two large cytotaxonomic groups, differing in the morphology of the sex chromosomes (JOTTERAND, 1972). The sex chromosomes of the first group are primitively acrocentric. In the second group, both primitive X and Y chromosomes have been translocated onto a pair of autosomes. Subsequent analyses showed that three different pairs of autosomes were involved in the Robertsonian translocation event (JOTTERAND-BELLOMO, 1986; 1988). A definite taxonomic revision will require multidisciplinary studies integrating molecular, cytogenetics, morphological and morphometrics analyses. In addition, the distributional extent of chromosomal polymorphism and of the different cytotypes through differential staining and *in situ* hybridisation still needs to be elucidated to provide a clear assessment of patterns of chromosomal evolution in this group.

Nannomys sp. Rongai – A (*minutoides* complex), Nairobi (♂KE106, ♂KE111, ♂KE144); Kenya. Species identification was possible by analysing the skull and cytochrome *b* phylogeny (unpublished data). The karyotype of this species is 2n=22, FN=36. The autosomes are constituted by six pairs of metacentrics and four pairs of acrocentrics; the X chromosome is a large metacentric and the Y a large submetacentric (Fig. 6A). This karyotype is presented here for the first time. The morphology of the sex chromosomes strongly suggests the fusion of the original sex chromosomes with a pair of autosomes, thus indicating the strict similarity of this karyotype to of *N. minutoides* from Zambia. Therefore, further banding analyses are needed to define relationships between these species within a wider taxonomic framework.

Nannomys sp. (*minutoides* complex), Mutanda Research Station, Mutoma, Solwezi (♂ZM8, ♀ZM16, ♀ZM24); Zambia. The chromosomal complement was 2n=25 in a male and a female, while another female had 2n=24. However, the NF is 36 in all specimens. The karyotype is composed of five large metacentric chromosomes, and six pairs of acrocentrics decreasing in size. The heterochromosomes are fused with an autosome. In both females studied, one of the X chromosomes showed a partial deletion, thus resembling the Y in size. This karyotype differs significantly from the one reported by JOTTERAND (1972) from Kafue (Zambia, Lusaka region), characterized by a 2n=34 with all-acrocentric autosomes. The reduction in diploid number (2n=24-25), together with the maintenance of the FN and the occurrence of large biarmed chromosomes is due to the presence of Rb fusions (for identification, see CASTIGLIA et al., 2002a). The high chromosomal diversification of the Zambian samples together with the occurrence of "all-acrocentrics" and Rb populations in other areas confirm the extensive chromosomal variability of this taxon (MATTHEY, 1964). As the type locality for the species is Cape Town (South Africa), the attribution of these specimens (including those reported by JOTTERAND, 1972) to this species is therefore questionable.

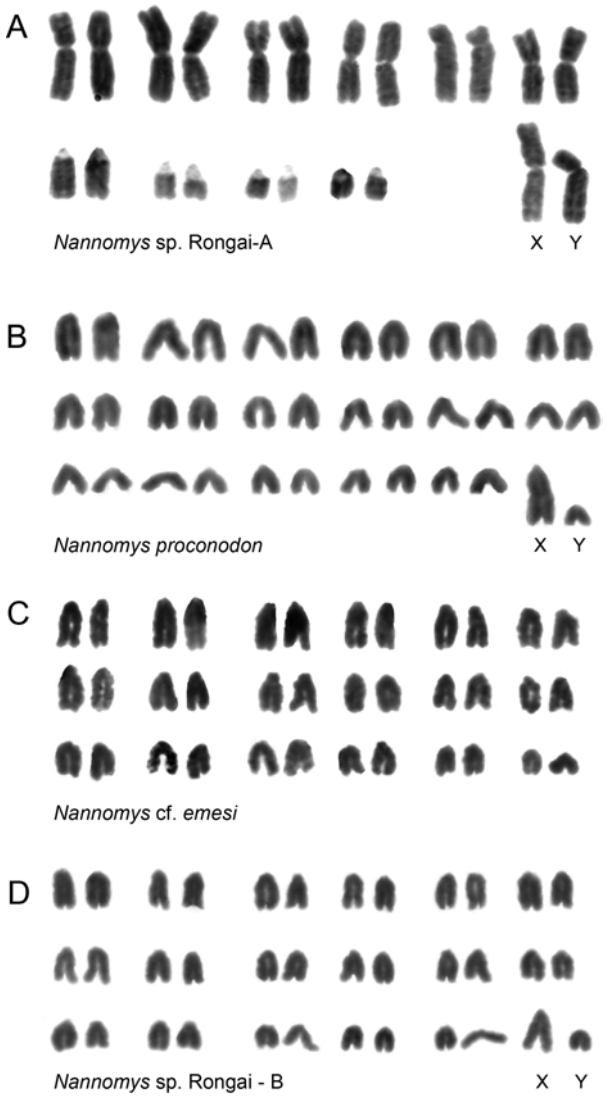

Fig. 6. – A) The karyotype of *Nannomys sp.* Rongai – A (*minutoides complex*), 2n=22, FN=36, X Y. B) The karyotype of *Nannomys proconodon*, 2n=36 and NFa=34, X Y. C) The karyotype of *Nannomys* cf. *emesi*, 2n=36, FN=36. D) The karyotype of *Nannomys* sp. Rongai – B, 2n=36, NFa=34, X Y.

– *Nannomys proconodon* (Rhoads, 1896).

Zeway (♂ET105, ♂ET113); Ethiopia. The karyotype is characterized by 2n=36 and NFa=34. All chromosomes are acrocentrics decreasing in size. The X chromosome is a large acrocentric with Y being small (Fig. 6B). This species was identified in Ethiopia by YALDEN et al. (1976) on the basis of skull measurements. It was considered a synonym of *M. setulosus* by MUSSER & CARLETON (1993) and confirmed hesitantly by YALDEN et al. (1996). The

type locality is Sheikh Hussein, Ethiopia (East of the Rift Valley, at the same latitude of Zeway), and the species seems to occur in the same habitats as *N. tenellus*, i.e. from lowland forests to arid savannas.

Nannomys cf. *emesi.* Kitale (♀KE117); Kenya. The chromosomal complement is 2n=36, FN=36. All chromosomes are acrocentrics decreasing in size (Fig. 6C). The sex chromosomes have been not yet identified. This karyotype is presented here for the first time, and is very similar in morphology *N. proconodon*. The identification of the species was based on skull measurements. *N. emesi* was considered synonymous of *M. mahomet* by MUSSER & CARLETON (2005), who underlined that the series of *emesi* could not be distinguished from the large samples of *mahomet* collected by Osgood in Ethiopia.

Nannomys sp. Rongai – B. (♀KE107, ♂KE136, ♀KE140); Kenya. This species carries the same "all acrocentric" karyotype (2n=36, NFa=34; Fig. 6D) as *N. cf. emesi,* but there are important differences in the external body morphology, the specimens from Kitale being much smaller than those from Rongai. No species assignment for the moment has been attempted for these specimens. This karyotype is presented here for the first time. The X and the Y chromosomes are large and medium size acrocentrics, respectively.

– *Mastomys* (Thomas, 1915).

The species of this genus are widespread in the African continent where they represent an important component of the rodent fauna and constitute a serious problem for agriculture and human plague (SINGLETON et al., 1999). However, their taxonomy has been subject to discussion for a long time. Several papers (GREEN et al., 1980; HUBERT et al., 1983; CHEVRET et al., 1994; BRITTON-DRAVIDIAN et al., 1995; GRANJON et al., 1996; GRANJON et al., 1997; LECOMPTE et al., 2002; VOLOBOUEV et al., 2002b; COLANGELO et al., in prep.), employing cytogenetic, morphological and molecular approaches, have assessed the monophyly of the genus and clarified the phylogenetic relationships within the genus and what was considered the *Praomys sensu lato* group. However, the most recent morphological and cytogenetic studies have indicated the possible occurrence of sibling species and/or new cryptic species (LAVRENCHENKO et al., 1998; VOLOBOUEV et al., 2001; 2002b).

The four species *M. natalensis*, *M. huberti*, *M. coucha*, *M. erythroleucus* are phylogenetically closely related, while the taxonomical and systematic position of the other taxa included in the genus is still uncertain (GRANJON et al., 1997; LECOMPTE et al., 2002).

The available karyotypic data are as follows. The diploid number of *M. natalensis* is 32 and the NFa varies from 52 to 54 across the distribution range; this is the most representative species, and occurs in sub-Saharan Africa. *M. huberti* has the same diploid number as *M. natalensis* (2n=32) but the NFa ranges from 44 to 46 (DUPLANTIER et al., 1990; GRANJON et al., 1997); the range is restricted to Mauritania, Mali, Burkina Faso and Senegal (GRANJON et al., 1997). *M. coucha* has been described from southern Africa (RSA and Zimbabwe) and presents 2n=36 and NFa=52-54 (LYONS et al., 1980; LEE & MARTIN, 1980; GREEN et al., 1980); however, HALLET (1979) reported additional NFa variability (54 – 56). *M. erythroleucus* ranges from Senegal to Ethiopia and Uganda and shows 2n=38; the NFa varies from 40 to 60. However, the comparison of the G-banded karyotypes and cytochrome *b* based phylogeny suggests that the specimens showing NFa=40 represent a separate species (VOLOBOUEV et al., 2002b), while the taxonomic status of the other cytotypes (NFa=50, NFa=52-53 and NFa=60) remains uncertain (VOLOBOUEV et al., 2001; 2002b). *M. shortridgei* occurs in the extreme northwest of Botswana and in northeast Namibia. GORDON (1985) reported in Namibia a karyotype with 2n=36 and NFa=50.

QUMSIYEH et al. (1990) reported a karyotype with 2n=32 and NF=50-54 from Kenya which they considered to be different from *M. natalensis* and that attributed to *M. hildebrandtii*. This karyotype was considered by QUMSIYEH et al. (1990) to be similar to the one described by CAPANNA et al. (1982) in Somalia as *M. huberti*, although there was no comparison with type material. QUMSIYEH et al. (1990) argued that *M. hildebrandtii* (type locality Ndi, Tahita Hills, in Kenya) is an older name for *M. huberti* (type locality Zungeru, N. Nigeria). However, the karyology for the West African specimens assigned to *huberti* (2n=32, FN=44) is different from that of the Kenyan specimens that QUMSIYEH et al. (1990) considered to be *hildebrandtii* (2n=32, FN=50-54). Therefore, GRANJON et al. (1997) claimed that these taxa are not synonyms and *M. huberti* is a different species, even though specimens from the type region have not yet been investigated karyologically and the type locality lies outside the distribution range of what is currently called *M. huberti* (GRANJON et al., 1997). For the time being there is no indication that *hildebrandtii* (with a type locality in southern Kenya) is different from *M. natalensis.* Therefore, while waiting for a definitive comparison with the karyotypes from type localities, *M. hildebrandtii* should be considered only as a younger synonym of *M. natalensis.*

Finally, LAVRENCHENKO et al. (1998) described a new species from the Awash Valley (Ethiopia) and named it *M. awashensis*; its diploid number is 32 and the NFa is 54, but it differs form *M. natalensis* in chromosome morphology and C-banding pattern.

Three different chromosomal formulas have been found in our samples. The more common karyotype shows 2n=32 and NFa=52-54 and here has been attributed to *M. natalensis*. However, one specimen collected in Ethiopia (Zeway) shares the same 2n=32 and NFa=54 karyotype, but was found not to be closely related phylogenetically to *M. natalensis* on the basis of the analysis of cytochrome *b* sequences (COLANGELO et al., in prep). Therefore, in absence of further comparisons, it is here provisionally referred to *M. awashensis* described in Ethiopia by LAVRENCHENKO et al. (1998).

– *Mastomys natalensis* (Smith, 1834).

Nairobi (♂KE142), Kitale (♀KE123); Kenya. Matongolo (♂T50012), Morogoro (♀T50198, ♀T50199, ♂T50200), Singida (♀T50197); Tanzania. Mutoma, Meheba (♀ZM2, ♀ZM5, ♂ZM34, ♀ZM36, ♀ZM38); Zambia. All the karyotypes show 2n=32 and both NFa=52 and 54 were found. The most common karyotype is composed of 12 pairs of biarmed chromosomes of

decreasing size and three pairs of acrocentrics. The X chromosome is a large submetacentric, and the Y chromosome is a large acrocentric. This karyotype is comparable to those described for *M. natalensis* from other localities (Matthey, 1955, 1966a, b; Capanna et al., 1982; Hubert et al., 1983; Orlov et al., 1989; Duplantier et al., 1990; Baskevich & Orlov, 1993; Leirs, 1994; Britton-Davidian et al., 1995; Codja et al., 1996; Fadda et al., 2001).

Fig. 7. – The karyotype of *Mastomys erythroleucus*, Zeway, Ethiopia 2n=38, NFa=53-54, X Y. Note the heteromorphic condition of one of the smallest metacentrics.

– *Mastomys* cfr. *awashensis* (Lavrenchenko et al., 1998).

Zeway (ET102♂); Ethiopia. The karyotype presents the same chromosomal formula as *M. natalensis* (2n=32 and NFa=54) and is composed of thee pairs of acrocentrics and twelve pairs of biarmed chromosomes, six of which are metacentrics and six subtelocentrics. The X and the Y chromosomes are submetacentrics, the former being medium-large and the latter medium-small. A preliminary G-banding analysis (the complete comparison will appear elsewhere) has shown differences probably due to deletions and/or additions in the autosomal complement. According to the cytochrome *b* sequences (Colangelo et al., in prep), this specimen is not related to the *M. natalensis* clade. Therefore, there is strong evidence suggesting that this taxon represents a separate species from *M. natalensis.* Further analysis will probably confirm the attribution of this taxon to *M. awashensis*.

– *Mastomys erythroleucus* (Temminck, 1953).

Rongai (♂KE101, ♂KE115, ♀KE132); Kenya. Zeway (♀ET128, ♂ET122, ♂ET128); Ethiopia. The Kenyan karyotype consists of 12 pairs of biarmed and six pairs of acrocentric chromosomes. The X chromosome is a medium size submetacentric and the Y is a small submetacentric. The Ethiopian karyotype is represented by 17-18 biarmed and 19-20 acrocentric chromosomes. The X is a large submetacentric and the Y is a small subtelocentric (Fig. 7). All the samples show the typical *M. erythroleucus* diploid number (2n=38). However, the Ethiopian and Kenyan specimens differ in NFa which is 52-53 in the former and 60 in the latter. A wide variability in NFa has been reported from other East and West African localities, with numbers ranging from 40 up to 60 (Matthey, 1965b; 1966a; 1967; Kral, 1971; Tranier, 1974; Hubert et al., 1983; Viegas-Péquignot et al., 1987; Orlov et al., 1989; Britton-Davidian et al., 1995; Codja et al., 1996; Bulatova et al., 2002; Volobouev et al., 2001; 2002a). According to the analysis of cytochrome b (Colangelo et al., in prep.) the genetic divergence between these two cytotypes it is very low in spite of the remarkable NFa variation.

– *Stenocephalemys* (Frick, 1914).

The genus now includes the three Ethiopian endemic species *S. albocaudata, S. albipes* and *S. griseicauda* (Musser & Carleton, 2005). It has been recognised recently, on the basis of cytogenetic, molecular and morphometric data (Chevret et al., 1994; Corti et al., 1995, 1999; Fadda et al., 2001; Lavrenchenko et al., 1999; Lecompte et al., 2002) that they constitute a monophyletic assemblage phylogenetically related to species of *Praomys, Mastomys, Myomyscus, Heimyscus,* and *Hylomyscus* (Lecompte et al., 2002). These studies have also shown that *S. albipes* should not be referred to *Myomys albipes* or *Praomys* (Misonne, 1969; Qumsiyeh et al., 1990; Yalden et al., 1976).

This genus has long been considered taxonomically confused, as it was included in a group of genera together with *Praomys*, *Mastomys*, *Hylomyscus*, *Colomys* and *Stenocephalemys* which are closely related (Chevret et al., 1994). There are available cytogenetic data for *S. albipes,* 2n=46 and NFa=50-53 (various localities in Ethiopia), S. *albocaudata* (2n=54, NFa=60) and *S. griseicauda* (2n=54, NFa=54) (Corti et al., 1999).

– *Stenocephalemys albipes* (Rüppell, 1842).

Mugo (♂ET108, ♂ET109, ♂ET111, ♀ET121, ♀ET123); Ethiopia. The species is widespread all over Ethiopia in forest blocks at altitudes ranging from 800 m up to 3300 mt a.s.l. (Yalden et al., 1976; Afework Bekele & Corti, 1997). The diploid number is 46 and the NFa is 50-53 (Fig. 8). The X is a large submetacentric and the Y (not shown) a medium size metacentric. All karyotypes are composed of 4 pairs of large biarmed chromosomes, 17 pairs of acrocentric chromosomes decreasing in size (on some of them very small arms are visible), and of one pair of small biarmed chromosomes. The chromosome pair numbers 1 and 3 are polymorphic (the latter not shown), i.e. they are found either as acrocentrics or submetacentrics due to a pericentric inversion. Corti et al. (1999) described the karyotype of this species from other localities in Ethiopia, and found the same diploid number and the same variation in NFa (50-53), due to the occurrence of a polymorphism. It is interesting to note that the polymorphism found in Zeway involves the same autosomes as those described by Corti et al. (1999) except for one specimen (ET123) that showed a polymorphism involving the largest chromosome pair (n° 1) of the entire autosomal set (Fig. 8).

Fig. 8. – The karyotype of *Stenocephalemys albipes*. 2n=46, NFa=50-53, X X. Note the heteromorphic condition of the largest autosome.

– *Grammomys* (Thomas, 1915).

The genus includes 12 species (MUSSER & CARLETON, 2005). The species cytogenetically studied so far show a wide variation in B chromosomes. CIVITELLI et al. (1989) described specimens of *G. gazellae* (synonym of *G. macmillani)* from Central Africa 2n=56-71, with 2-17 B chromosomes. The occurrence of B-chromosomes as well as Robertsonian fusions has been documented by ROCHE et al. (1984) in five specimens (a mother and four pups) of *G. dolichurus* from Somalia (2n=54-61, NFa=70-75).

MATTHEY (1971) described the karyotype of *G. surdaster* from Katanga (2n=52; NFa=62). FADDA et al. (2001) found a karyotype in the Maasai steppe with 2n=27 and NFa=39 that could not be allocated to any species. They maintained that, after craniological and craniometrical comparison with extensive Tanzanian material including most of the relevant type-specimens, the taxonomic situation of the *Grammomys-Thamnomys* complex of this part of Africa is yet to be established. More recently, on the basis of 16S rRNA gene analyses of extensive samples, VERHEYEN et al. (2003) reported the occurrence, in this part of Africa, of at least three species complexes, i.e. *G. macmillani, G. dolichurus* and *G. surdaster.* Taxonomic attribution made here is based on morphological comparison with larger series and mtDNA analysis (VERHEYEN et al., 2003), but apart from including the cytotype in a species group, no definitive allocation or new classification was possible.

– *Grammomys* sp. *surdaster* (Thomas and Wroughton, 1908) complex.

Mutanda Research Station (♂ZM25, ♀ZM14); Zambia. The diploid number is 2n=51 in the male and 2n=50 in the female and the NFa is 61 (Fig. 9A). The difference between the male and female depends on a structural Robertsonian fusion in the former concerning the largest metacentric (not shown in the figure). The autosomes are represented by one pair of large metacentric chromosomes, a heteromorphic pair formed by a small metacentric and a small acrocentric, five pairs of small metacentrics, and 17 pairs of acrocentrics decreasing in size (Fig. 9A). There are two different X configurations: a submetacentric (in the male) and a subtelocentric occurring together with the submetacentric (in the female). The Y chromosome is a small subtelocentric (not shown). This karyotype is presented here for the first time, but it resembles the one described from Katanga by MATTHEY (1971).

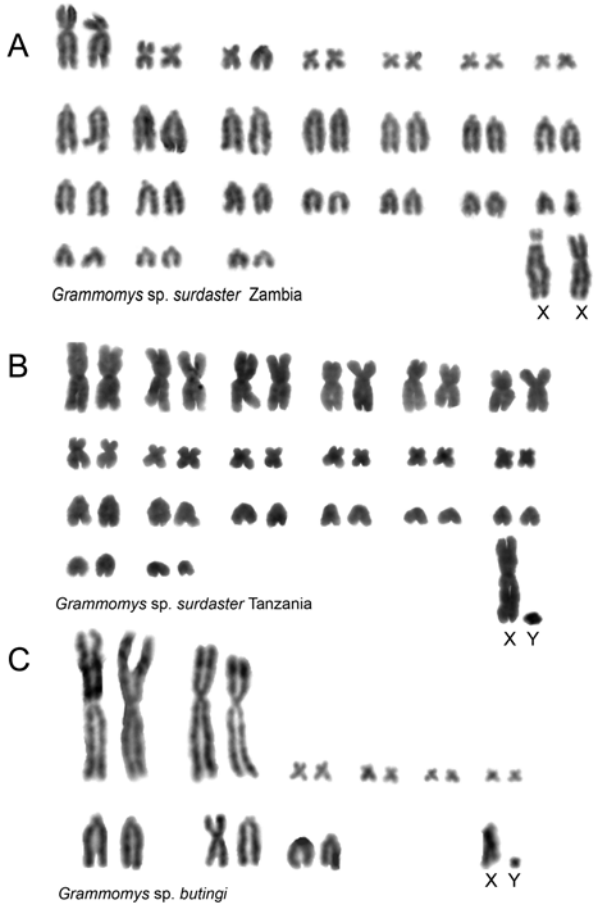

Fig. 9. – A) The karyotype of *Grammomys* sp. *Surdaster* (Zambia), 2n=50-51, NFa=61, X X. Note the heteromorphic condition of one of the smallest metacentrics an of the X. B) The karyotype of *Grammomys* sp. *surdaster* (Tanzania), 2n=42, NFa=64, X Y. C) The karyotype of *Grammomys* sp. *butingi*, 2n=20, NFa=31, X Y. Note the heteromorphic condition of one of the medium size chromosomes.

Grammomys sp. *surdaster* complex Kitundu Forest, Uluguru Mt. range (♂T50235, ♀T50237); Tanzania. The karyotype is 2n=42, and the NFa is 64 (Fig. 9B). The karyotype comprises 12 pairs of biarmed chromosomes decreasing in size, from large to small, and 8 pairs of acrocentrics of medium to small size. The X is a large metacentric and the Y is the smallest acrocentric. This karyotype is presented here for the first time.

– *Grammomys* sp. *butingi* (Thomas, 1911 complex).

Jipe (♂T50485); Tanzania. The karyotype is characterized by 2n=20 and NFa=31. The autosomal set is represented by two pairs of very large metacentrics, two pairs of medium size subtelocentrics, a pair of medium size heteromorphic chromosomes (a metacentric and a subtelocentric) and four pairs of small metacentrics (Fig. 9C). The X chromosome is a medium size subtelocentric and the Y a small metacentric. This karyotype is presented here for the first time.

MYOXIDAE (Gray, 1821).

– *Graphiurus* (Smuts, 1832).

The systematic relationships and the taxonomy within the genus are at present not fully resolved (BENTZ & MONTGELARD, 1999; GENEST-VILLARD, 1978; SCHLITTER et al., 1985; HOLDEN, 1993; 1996). Revisions made over the last twenty years, all of which are exclusively based on size and morphology, have reached different conclusions: the number of species described varies from five (MEESTER & SETZER,1971) and six (GENEST-VILLARD, 1978), to fourteen (HOLDEN, 1993). More recently, MONGELARD et al. (2003) examined six taxa of *Graphiurus* through nuclear and mitochondrial genes, amongst which *G. microtis* from Tanzania. They showed that the low resolution found for the genus most probably accounts for their rapid diversification.

In general, the karyotypes of *Graphiurus* are characterized by the prevalence of biarmed autosomes (ZIMA et al., 1994), but diploid numbers are known for only a few species: *G. cf. parvus*, 2n=70 (DOBIGNY et al., 2002); *G. murinus*, 2n=70 (TRANIER & GAUTUN, 1979); *G. hueti*, 2n=40 (TRANIER & DOSSO, 1979). One should recall, however, that chromosomal variation is common in Myoxidae, as shown in the European *Eliomys* (FILIPPUCCI et al., 1988; 1990) and it would not be surprising to find an even larger one in *Graphiurus*.

Five individuals from three different localities were analyzed and their karyotypes are presented here. Because their taxonomy is still under discussion (the most recent checklist by HOLDEN, 1993, highlighted that taxonomic assignment must be considered provisional), we provide no definite specific allocation for our specimens. For the moment, we refer to them as belonging to *Graphiurus* cf. *murinus*, *Graphiurus* sp. 1 and *Graphiurus* sp. 2.

Graphiurus cf. *murinus*. Zeway (♀ET100, ♀ET 104, ♂ET106); Ethiopia. The karyotype is characterized by 2n=60 and NFa=76. The autosomal set is composed of a large pair of metacentrics, one medium size pair of metacentrics, four pairs of subtelocentrics of medium size, three pairs of medium to small metacentrics and 20 pairs of acrocentrics decreasing in size (Fig. 10A). The X chromosome is a large acrocentric and the Y a very small one. This karyotype is presented here for the first time. YALDEN et al. (1976) attributed to this species the "relative small number of records" for Ethiopia. The type locality of the species is the Cape of Good Hope, South Africa, but it is questionable whether this wide distribution reflects the occurrence of a single species.

Graphiurus sp. 1. Meheba (♂ZM6); Zambia. The diploid number is 2n=54 and NFa=78. The karyotype is composed of nine pairs of metacentric chromosomes decreasing in size (from the largest of the entire set to nearly the smallest), four pairs of subtelocentrics, and 13 pairs of acrocentrics decreasing in size (from the second in size of the entire set to the smallest one) (Fig. 10B). The X chromosome is a medium size metacentric, and the Y is the smallest element of the set. This karyotype is presented here for the first time.

Graphiurus sp. 2. Chunya (♂TZ506); Tanzania. Unfortunately the quality of the preparations is only sufficient for a general description of the karyotype. The 2n is 50 and the NFa is 66. The karyotype is composed of nine pairs of metacentrics decreasing in size and 15 pairs of acrocentrics decreasing in size (Fig. 10C). Both the X and the Y are acrocentrics but the former is the largest one of the complement and the latter is very small. This karyotype is presented here for the first time.

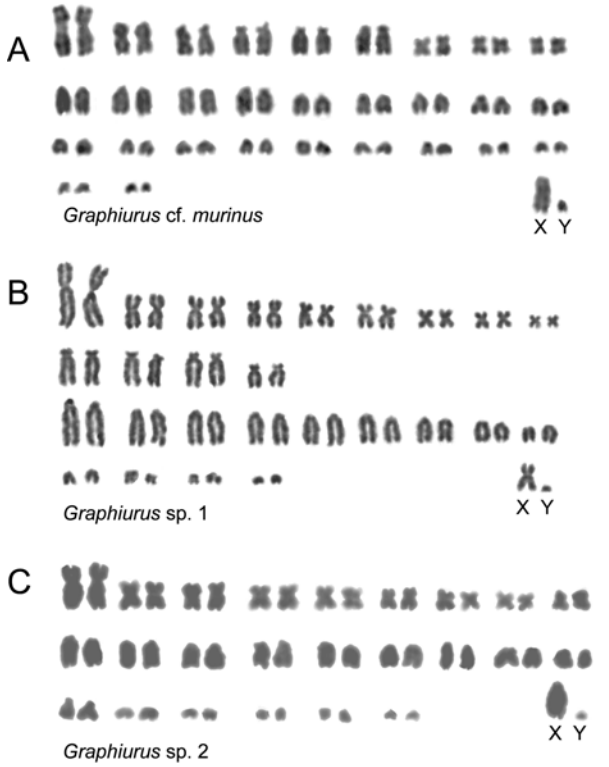

Fig. 10. – A) The karyotype of *Graphiurus* cf. *murinus*, 2n=60, NFa=76, X Y. B) The karyotype of *Graphiurus* sp. 1 (Zambia), 2n= 54, NFa=78, X Y. C) The karyotype of *Graphiurus* sp. 2 (Tanzania), 2n=50, NFa=66, X Y.

DISCUSSION

The number of karyotypes discussed here totals 37. Seventeen are described here for the first time. For four species or species complexes, we report chromosomal variants and for sixteen karyotypes additional localities of occurrence. Some of the karyotypes characterize taxa that have been either fully accepted by the most recent checklists or need taxonomic re-evaluation or a new description. The latter are *Cricetomys* cf. *gambianus, Saccostomus* cf. *elegans*, *Gerbilliscus nigricaudus, G.* cfr. *muansae, Arvicanthis* (ANI-5 and ANI-6), *A. nairobae*, *Acomys selousi*, *Lemniscomys zebra, L.* cf. *striatus massaicus, Nannomys proconodon, Nannomys* cf. *emesi, Nannomys* sp., *Grammomys surdaster*, *Grammomys* sp.1 and sp. 2, *Graphiurus* cf. *murinus, Graphiurus* sp. 1 and sp. 2. In all other cases, as the karyotypes have been or will be described elsewhere, we have reported the occurrence of chromosomal variants, new sampling sites or have provided a more precise taxonomic attribution. Fur-

thermore, we have highlighted problems in taxonomy, due to the occurrence of sibling and cryptic species or species complexes, for which further detailed analyses are needed.

There is a general pattern emerging from this report that confirms all recent suggestions regarding African rodent taxonomy and systematics researchers, i.e. biodiversity is much higher than has been previously estimated, at least that revealed by cytogenetics, so that the list of 386 species (MUSSER & CARLETON, 1993) will increase rapidly. This is true for the all genera investigated, with the exception of *Aethomys*, for which there was no apparent problem of taxonomic attribution at species level, but for which karyotypes are known from a limited number of localities (one only for *A. kaiseri*) and variants cannot be excluded a-priori.

However, it is difficult to state whether the chromosomal variants detected warrant a different species attribution in all cases. For many this is undoubtedly true. *Acomys* cf. *selousi*, *Arvicanthis* ANI-5, *Arvicanthis* ANI-6, *Nannomys tenellus*, *N. proconodon*, *N.* cf. *emesi, Nannomys* sp. (Rongai), *Grammomys* sp.1 and sp. 2 represent cases that would strongly suggest a specific attribution. For others, it would be premature to do so until more extensive analyses have been performed, possibly including estimates of gene flow between cytotypes. For example, the different karyotypes of *Cricetomys* cf. *gambianus* found in West (GRANJON et al., 1992; CODJA et al., 1994) and East Africa could correspond to different biological species or represent extremes of some form of chromosomal variation. Nonetheless, these data and parallel analyses suggest that at least seven specific names that were not included in MUSSER & CARLETON's (1993) checklist need to be restored and accepted at the full species rank. These are *Saccostomus* cf. *elegans*, *Gerbilliscus* cfr. *muansae*, *Acomys* cf. *selousi*, *Lemniscomys* cf. *zebra*, *Nannomys proconodon*, *N.* cf. *emesi* and *Grammomys surdaster.*

Within species chromosomal variation is a common phenomenon in rodents (recent literature is rich in references; see, for example, those cited here for *Arvicanthis*) and the cases we report here of the *Stenocephalemys albipes* and *Saccostomus* cf. *elegans* are evident examples. These could represent instances of raciation but, for the moment, this is impossible to establish. On the contrary, the cytotypes of the *Arvicanthis niloticus* complex (Zeway, Kitale, ANI-5) clearly suggest a process of divergence in action that might have reached full speciation as suggested by the analysis of the cytochrome b mitochondrial gene (CORTI et al., submitted). However, we are cautious when considering most of the taxa studied here, as we believe that extensive comparisons with type material using a multidisciplinary approach is needed before reaching a definite taxonomic conclusion.

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REFERENCES

AFEWORK BEKELE, E. CAPANNA, M. CORTI, L.F. MARCUS & D.A. SCHLITTER (1993). Systematics and geographic variation of Ethiopian *Arvicanthis* (Rodentia, Muridae). *J. Zool., Lond*., 230: 117-134.

AFEWORK BEKELE & M. CORTI (1997). Forest blocks and altitude as indicators of *Myomys albipes* (Mammalia: Rodentia) distribution in Ethiopia. *Trop. Zool*., 10: 287-293.

ALLEN, G.M. (1939). *A checklist of African mammals*. Bulletin of the Museum of Comparative Zoology at Harvard College, 83: 1-763.

BAKER, R.J., M.B. QUMSIYEH & I.L. RAUTENBACH (1988). Evidence for eight tandem and five centric fusions in the evolution of the karyotype of *Aethomys namaquensis* A. Smith (Rodentia: Muridae). *Genetica*, 76: 161-169.

BAROME, P.-O., M. MONNEROT & J.-C. GAUTUN (1998). Intrageneric phylogeny of *Acomys* (Rodentia, Muridae) using mitochondrial gene cytochrome *b. Mol. Phyl. Evol*., 9: 560-566.

BAROME, P., V. VOLOBOUEV, M. MONNEROT, J. MFUNE, W. CHITAKAULI, J.C. GAUTUN & C DENYS (2001). Phylogeny of *Acomys spinosissimus* (Rodentia, Muridae) from north Malawi and Tanzania: evidence from morphological and molecular analysis. *Biol. J. Linn. Soc*., 738: 321-340.

BASKEVICH, M.I. & L.A. LAVRENCHENKO (2000). Review of karyological studies and the problems of systematics of Ethiopian *Arvicanthis* Lesson, 1842 (Rodentia: Muridae). *Bonn. zool. Monogr.*, 46: 209-215.

BASKEVICH, M.I. & V.N. ORLOV (1993). Karyological differentiation of rats of the genus *Mastomys* (Rodentia, Muridae) from the central part of Ethiopian Rift Valley. *Zool. Zhur*., 72: 112-121.

BATES, P.J.J. (1988). Systematics and zoogeography of *Tatera* (Rodentia: Gerbillinae) of north-east Africa and Asia. *Bon. Zool. Beitr.* 39: 265-303.

BENAZZOU, T., E. VIEGAS-PÉQUIGNOT, M. PROD'HOMME, M. LOMBARD, F. SETTER, B. DUTRILLAUX (1984). Chromosomal phylogeny of Gerbillidae. III. Species study of the genera *Tatera, Taterillus, Psammomys and Pachyuromys*. *Ann. Genet*. 27: 17–26.

BENTZ, S. & C. MONTGELARD (1999). Systematic position of the African dormouse *Graphiurus* (Rodentia, Gliridae) assessed from Cytochrome *b* and 12S rRNA mitochondrial genes. *J. Mamm. Evol*., 6: 67-83.

BREED, W.G., G.A. COX, C.M. LEIGH & P. HAWKINS (1988). Sperm head structure of a murid rodent from southern Africa: the red veld rat *Aethomys chrysophilus*. *Gamete Res*., 19: 191-202.

BRITTON-DAVIDIAN, J., J. CATALAN, L. GRANJON & J.M. DUPLANTIER (1995). Chromosomal phylogeny and evolution

in the genus *Mastomys* (Mammalia, Rodentia). *J. Mamm*., 76: 248-262.

Bulatova, N., L. Lavrenchenko, V. Orlov & A. Milishnikov (2002). Notes on chromosomal identification of rodent species in western Ethiopia. *Mammalia*, 66: 128-132.

Capanna, E., M.V. Civitelli & A. Ceraso (1982). Karyotypes of Somalian rodent populations. 3. *Mastomys huberti* (Wroughton, 1908) (Mammalia Rodentia). *Mon. Zool. It.,* 5: 141-152.

Capanna, E., M.V. Civitelli & M.G. Filippucci (1985). Karyology of 11 species of African Rodents. IV Int. Ther. Cong., Edmonton, Canada, Aug. 13-20.

Capanna, E. & M.V. Civitelli (1988). A cytotaxonomic approach to the systematics of *Arvicanthis niloticus* (Desmarest 1822) (Mammalia Rodentia). *Trop. Zool*., 1: 29-37.

Capanna, E., Afework Bekele, M. Capula, R. Castiglia, M.V. Civitelli, J-Cl. Codja, M. Corti & C. Fadda (1996). A multidisciplinary approach to the systematics of the genus *Arvicanthis*, Lesson 1842 (Rodentia, Muridae). *Mammalia,* 60: 677-696.

Capanna, E., J.C. Codjia, C. Chrysostome & M.V. Civitelli (1997). Les chromosomes des rongeurs du Benin (Afrique de L'Ouest): 3. Murinae. *Rend. Fis. Acc. Lincei,* 8: 25–37.

Capula, M., M.V. Civitelli, M. Corti, Afework Bekele & E. Capanna (1997). Genetic divergence in the genus *Arvicanthis* (Rodentia: Murinae). *Biochem. Syst. Ecol*., 25: 403-409.

Carleton, M.D. & E. Van der Straeten (1997) Morphological differentiation among Subsaharan and North African populations of the *Lemniscomys barbarus* complex (Rodentia: Muridae). *Proc. Biol. Soc. Washington,* 110: 640–680.

Castiglia, R., E. Gornung & M. Corti (2002a). Cytogenetic analyses of chromosomal rearrangements in *Mus minutoides / musculoides* from North-West Zambia through mapping of the telomeric sequences (TTAGGG)n and Banding techniques. *Chromosome Res.*, 10: 399-406.

Castiglia, R., C. Fadda, M. Corti, A. Scanzani, W. Verheyen & E. Capanna (2002b). Chromosomal evolution in the African Arvicanthine rats (Murinae, Rodentia): comparative cytogenetics of *Lemniscomys* (*L. zebra, L. rosalia, L. striatus*) and *Arvicanthis dembeensis*. *J. Zool. Syst. Evol. Res*., 40: 223-231.

Castiglia, R., M. Corti, P. Colangelo, F. Annesi, E. Capanna, W. Verheyen, A. Sichilima & R. Makundi (2003a). Chromosomal and molecular characterization of *Aethomys kaiseri* from Zambia and *Aethomys chrysophilus* from Tanzania (Rodentia, Muridae). *Hereditas*, 139: 81-89.

Castiglia, R., M. Corti, Tesha Protas, A. Scanzani, C. Fadda, E. Capanna & W. Verheyen (2003b). Cytogenetics of the genus *Arvicanthis* (Rodentia, Muridae). 3. Comparative cytogenetics of *A. neumanni* and *A. nairobae* from Tanzania. *Genetica*, 118: 33-39.

Castiglia, R., Afework Bekele, R. Makundi, N. Oguge & M Corti (2006). Chromosomal diversity in the genus *Arvicanthis* from the horn and east Africa. A taxonomic and Phylogenetic evaluation. *J. Zool. Syst. Evol. Res*. In press.

Chevret, P., L. Granjon, J.M. Duplantier, C. Denys & F. Catzeflis (1994). Molecular phylogeny of the *Praomys* complex (Rodentia: Murinae): a study based on DNA/DNA hybridization experiments. *Zool. J. Linn. Soc*., 112: 425-442.

Chevret, P. & G. Dobigny (2005). Systematics and evolution of the subfamily Gerbillinae (Mammalia, Rodentia, Muridae). *Mol. Phyl. Evol*., 35: 674–688.

Chimimba, C.T. (1998). A taxonomic synthesis of southern African *Aethomys* (Rodentia: Muridae) with a key to species. *Mammalia*, 62: 427-437.

Chimimba, C.T., N.J. Dippenaar & T.J. Robinson (1999). Morphometric and morphological delineation of southern African species of *Aethomys* (Rodentia: Muridae). *Biol. J. Linn. Soc*., 67: 501-527.

Civitelli, M.V., P. Consentino & E. Capanna (1989). Inter- and intra-individual chromosome variability in *Thamnomys* (*Grammomys*) *gazellae* (Rodentia, Muridae). B-chromosomes and structural heteromorphisms. *Genetica*, 79: 93-105.

Civitelli, M.V., R. Castiglia, J.-Cl. Codja & E. Capanna (1995). Cytogenetics of the genus *Arvicanthis* (Rodentia, Murinae). 1. *Arvicanthis niloticus* from Republic of Benin (West Africa). *Z. Säugetierkunde*, 60: 215-225.

Codja, J.T.Cl., C. Chrysostome, M.V. Civitelli & E. Capanna (1994). Les chromosomes des Rongeurs du Bénin (Afrique de l'Ouest): 1. Cricetidae. *Rend. Fis. Acc. Lincei*, s. 9, v. 5: 277-287.

Codja, J.T.Cl., M.V. Civitelli, D. Bizzoco & E. Capanna (1996). Les chromosomes de *Mastomys natalensis* et *Mastomys erythroleucus* du Sud Bénin (Afrique de l'Ouest): nouvelles précisions sur la variabilité chromosomique. *Mammalia*, 60: 299-303.

Colangelo, P., M.V. Civitelli & E. Capanna (2001). Morphology and chromosomes of *Tatera* Lataste 1882 (Rodentia Muridae Gerbillinae) in West Africa. *Trop. Zool*. 14: 243–253.

Colangelo, P., M. Corti, E. Verheyen, F. Annesi, N. Oguge, R.H. Makundi & W. Verheyen (2005). Mitochondrial phylogeny reveals differential modes of chromosomal evolution in the genus *Tatera* (Rodentia: Gerbillinae) in Africa. *Mol. Phylogenet. Evol*., 35: 556–568.

Colangelo, P., L. Granjon, P.J. Taylor & M. Corti. Evolutionary systematics in African Gerbilline rodents (g. *Gerbilliscus* and *Gerbillurus*): inference from mitochondrial genes. Submitted.

Corbet, G.B. (1990). The relevance of metrical, chromosomal and allozyme variation to the systematics of the genus *Mus*. *Biol. J. Linn. Soc*., 41: 5-12.

Corbet, G.B. & J.E. Hill (1991). *A world list of mammalian species*. Oxford: Oxford Univ. Press.

Corti, M. (2002). Rodent taxonomy at the end of the 20th century. Delectatur musica. *Bull. Inst. Roy. Sci. Nat. Belg., Biologie,* 71: 17-33.

Corti, M., M.V. Civitelli, Afework Bekele, R. Castiglia & E. Capanna (1995). The chromosomes of three endemic rodents of the Bale mountains, South Ethiopia. *Rend. Fis. Acc. Lincei*, s. 9, v. 6: 157-164.

Corti, M., M.V. Civitelli, R. Castiglia, Afework Bekele & E. Capanna (1996). Cytogenetics of the genus *Arvicanthis* (Rodentia, Muridae). 2. The chromosomes of three species from Ethiopia*: A. abyssinicus, A. dembeensis* and *A. blicki*. Z. Säugetierkunde, 61: 339-351.

Corti, M. & C. Fadda (1996). Systematics of *Arvicanthis* (Rodentia, Muridae) from the Horn of Africa: a geometric morphometrics evaluation. *It. J. Zool*., 63: 185-192.

Corti, M., A. Scanzani, A.R. Rossi, M.V. Civitelli, Afework Bekele & E. Capanna (1999). Karyotypic and genetic divergence in the Ethiopian *Myomys-Stenocephalemys* complex (Mammalia, Rodentia). *It. J. Zool*., 66: 341-349.

Corti, M., R. Castiglia, F. Annesi & W. Verheyen (2004). Mitochondrial sequences and karyotypes reveal hidden diversity in African pouched mice (subfamily Cricetomyinae, genus *Saccostomus*). *J. Zool., London*, 262: 1–12.

Corti, M., F. Annesi, E. Verheyen & W. Verheyen Mitochondrial phylogeny and chromosomal evolution of *Arvicanthis* (Rodentia, Muridae). Submitted.

Davis, D.H.S. (1975). Genus *Aethomys*. In: Meester, J. & W.H. Setzer (eds), *The Mammals of Africa: an identification manual.* Part 6.6. Smithsonian Institution Press, Washington: 1-5.

Delany, M.J. (1975). *The rodents of Uganda*. London: Trustees of the British Museum (N.H.).

Denys, C. (1999). Of mice and men. Evolution in the East and South Africa during Plio-Pleistocene times. In: Bromage, T.G. & F. Schrenk (eds), *African biogeography, climate change, and human evolution*. Oxford University Press New York: 226-252.

Dippenaar, N.J. & I.L. Rautenbach (1986). Morphometrics and karyology of the Southern Africa species of the genus *Acomys* I. Geoffroy Saint-Hilaire, 1838 (Rodentia: Muridae). *Ann. of the Transvaal Museum*, 34: 129-183.

Dobigny, G., A. Nomao & J.-C. Gautun (2002). A cytotaxonomic survey of Rodents from Niger: implications for systematics, biodiversity and biogeography. *Mammalia,* 66: 495-523.

Dobzhansky, T. (1937). *Genetics and the origin of species*. Columbia University Press.

Ducroz, J.F. (1998). Contribution des approches cytogenetique et moleculaire a l'etude systematique et evolutive de genres de rongeurs Murinae de la 'division' *Arvicanthis*. *PhD Dissertation*. Museum National d'Histoire Naturelle, Paris.

Ducroz, J.F., L. Granjon, P. Chevret, J.M. Duplantier, M. Lombard & V. Volobouev (1997). Characterization of two distinct species of *Arvicanthis* (Rodentia, Muridae) in West Africa: cytogenetic, molecular and reproductive evidence. *J. Zool., Lond*., 241: 709-723.

Ducroz, J.F., V. Volobouev & L. Granjon (1998). A molecular perspective on the systematics and evolution of the genus *Arvicanthis* (Rodentia, Muridae): Inferences from complete cytochrome b gene sequences. *Mol. Phylogenet. Evol.*, 10: 104-117.

Ducroz, J.F., L. Granjon, M. Lombard & V. Volobouev (1999). Comparative chromosome analysis (R.- and C-Bands) of two South African murid species, *Lemniscomys rosalia* and *Rhabdomys pumilio* (Rodentia, Murinae). *Cytogenet. Cell Genet*., 87: 69–74.

Ducroz, J.F., V. Volobouev & L. Granjon (2001). An Assessment of the Systematics of Arvicanthine Rodents using Mitochondrial DNA sequences: Evolutionary and biogeographical implications. *J. Mammal. Evol*., 8: 173-206.

Duplantier, J.M., J. Britton-Davidian & L. Granjon (1990). Chromosomal characterization of three species of the genus *Mastomys* in Senegal. *Zeit. Zool. Syst. Evolut. forschung*, 28: 289-298.

Ellerman, J.R. (1941). *The families and genera of living rodents. Vol. II. Family Muridae*. British Museum (Natural History), London.

Ellerman, J.R., T.C.S. Morrison-Scott & R.W. Hayman (1953). *Southern African mammals 1758 to 1951: a reclassification*. London: British Museum (N.H.).

Fadda, C. & M. Corti (1998). Geographic variation of *Arvicanthis* (Rodentia, Muridae) in the Nile Valley. *Z. Säugetierkunde,* 63: 104-113.

Fadda, C. & M. Corti (2001). Geographic variation in *Arvicanthis* (Rodentia, Muridae) in the Nile Valley: a three dimensional geometric morphometrics evaluation. *Z. Säugetierkunde* , 63: 104-113.

Fadda, C., M. Corti & E. Verheyen (2001). Molecular phylogeny of *Myomys/Stenocephalemys* complex and its relationships with related African genera. *Biochem. Syst. Ecol*., 29: 585–596.

Fadda, C., R. Castiglia, P. Colangelo, R. Machang'u, R. Makundi, A. Scanzani, P. Tesha, W. Verheyen & E. Capanna (2001). The Rodent fauna of Tanzania 1: a cytotaxonomic report from the Maasai Steppe (1999). *Rend. Fis. Acc. Lincei*, s. 9, v12: 5-18.

Filippucci, M.G., M.V. Civitelli & E. Capanna (1986). The chromosomes of *Lemniscomys barbarus* (Rodentia, Muridae). *Boll. Zool*., 53: 355–358.

Filippucci, M.G., M.V. Civitelli & E. Capanna (1988). Evolutionary genetics of the dormouse, *Eliomys quercinus* Wagner, 1840. 1. Karyotype divergence. *Boll. Zool*., 55: 35-45.

Filippucci, M.G., F. Katzeflis & E. Capanna (1990). Evolutionary genetics and systematics of the garden dormouse, *Eliomys* Wagner, 1840 (Gliridae, Mammalia): 3. Further karyological data. *Boll. Zool*., 57: 149-152.

Fülling, O. (1992). Ergänzende Angaben über Gaumenfaltenmuster von Nagetieren (Mammalia: Rodentia) aus Kamerun. *Bonn. Zool. Beitr.*, 43: 415–421.

Gautun, J.-C., M. Tranier & B. Sicard (1985). Liste Preliminarie des rongeurs du Burkina-Faso (ex Haute-Volta). *Mammalia,* 49: 537–542.

Gautun, J.C., I. Sankhon & M. Tranier (1986). Nouvelle contribution à la connaissance des rongeurs du massif guinéen des monts Nimba (Afrique occidentale). Systématique et aperçu quantitatif. *Mammalia*, 50: 205-217.

Genest-Villard, H. (1967). Revision du genre *Cricetomys* (Rongeurs, Cricetidae). *Mammalia*, 31: 390-432.

Genest-Villard, H. (1978). Révision systématique du genre *Graphiurus* (Rongeurs, Gliridae). *Mammalia,* 42: 391-426.

Gordon, D.H. (1985). Cytogenetics of Shortridge's Mouse (*Mastomys shortridgei*) (Rodentia: Muridae) from southwest Africa/Namibia. *IV Ther. Cong. Edmonton, Canada*, August 13-20, 1985.

Gordon, D.H. (1986). Extensive chromosomal variation in the pouched mouse, *Saccostomus campestris* (Rodentia, Cricetidae) from Southern Africa: a preliminary investigation of evolutionary status. *Cimbebasia*, 8: 37-47.

Gordon, D.H. & I.L. Rautenbach (1980). Species complexes in medically important Rodents: chromosome studies of *Aethomys, Tatera*, and *Saccostomus* (Rodentia: Muridae, Cricetidae). *S. Afr. J. Sc.,* 76: 559-561.

Gordon, D.H. & C.R.B. Watson (1986). Identification of cryptic specie of rodents (*Mastomys, Aethomys, Saccostomus*) in the Kruger National Park. *South. Afr. J. Sci*., 21: 95-99.

Granjon, L., J.M. Duplantier, J. Catalan & J. Britton-Davidian (1992). Karyotypic data on Rodents from Senegal. *Isr. J. Zool*., 38: 106-111.

Granjon, L., J.M. Duplantier, J. Catalan, J. Britton-Davidian & G.N. Bronner (1996). Conspecificity of *Mastomys natalensis* (Rodentia: Muridae) from Senegal and South Africa: evidence from experimental crosses, karyology and biometry. *Mammalia*, 60: 697-706.

Granjon, L., J.M. Duplantier, J. Catalan & J. Britton-Davidian (1997). Systematics of the genus *Mastomys* (Thomas, 1915) (Rodentia: Muridae): a review. *Belgian J. Zool*., 127: 7-18.

Granjon, L. & G. Dobigny (2003). The importance of chromosomally-based identifications for correct understanding of African rodent zoogeography: Lake Chad murids as an example. *Mamm. Rev.*, 33: 77-91.

Green, C.A., H. Keogh, D.H. Gordon, M. Pinto & E.K. Hartwig (1980). The distribution, identification, and naming of the *Mastomys natalensis* species complex in southern Africa (Rodentia: Muridae). *J. Zool., London*, 192: 17-23.

Hallet, J.M. (1979). Chromosome polymorphism in *Praomys* (*Mastomys*) *natalensis* in Southern Africa: diploid studies. *South. Afr. J. Sci.,* 75: 413-415.

Holden, M.E. (1993). Family Myoxidae. In: Wilson, D.E. & D.M. Reeder D (eds), *Mammal species of the world. A taxonomic and geographic reference*. Smithsonian Institution Press, Washington D.C.: 763-770.

Holden, M.E. (1996). Systematic revision of Sub-Saharan African dormice (Rodentia: Myoxidae: *Graphiurus*) Part 1: an introduction to the generic revision, and a revision of *Graphiurus surdus*. *Am. Mus. Novitates*, 3157: 1-44.

Hubert, B. (1978). Revision of the genus *Saccostomus* (Rodentia, Cricetomyinae), with new morphological and chromo-

somal data from specimens from the lower Omo Valley, Ethiopia. *Bull. Carnegie Mus. Nat. Hist*., 6: 48-52.

HUBERT, B., F. ADAM & A. POULET (1973). Liste préliminaire des Rongeurs du Senegal. *Mammalia*, 37: 76-87.

HUBERT, B., F. MEYLAN, F. PETTER, A. POULET & M. TRANIER (1983). Different species in genus *Mastomys* from Western, Central and Southern Africa (Rodentia, Muridae). *Ann. Mus. Roy. Afr. Centr., Sc. Zool*., 237: 143.148.

HSU, T.C. & J.L. PATTON (1969). Bone marrow preparations for chromosome studies. In: BENIRSCHKE, K. (ed), *Comparative Mammalian Cytogenetics*. Springer-Verlag, Berlin: 454-460.

JOTTERAND, M. (1972). Le polymorphisme chromosomique des *Mus* (Leggadas) africains. Cytogenetique, zoogeographie, evolution. *Rev. Suisse Zool*., 79: 287-359.

JOTTERAND-BELLOMO, M. (1986). Le genre *Mus* africain, un exemple d'homogeneité caryotypique: etude cytogenetique de *Mus minutoides/musculoides* (Cote d'Ivoire) de *M. setulosus* (Republique Centrafricaine), et de *M. mattheyi* (Burkina Faso). *Cytogenet. Cell Genet*., 42: 99–104.

JOTTERAND-BELLOMO, M. (1988). Chromosome analysis of five specimens of *Mus bufo-triton* (Muridae) from Burundi (Africa): three cytogenetic entities, a special type of chromosomal sex determination, taxonomy, and phylogeny. *Cytogenet. Cell Genet*., 48: 88–91.

KING, M. (1993). *Species evolution, the role of chromosome change*. Cambridge: Cambridge University Press.

KRAL, B. (1971). Non-Robertsonian variability of karyotype in rats of the subgenus *Mastomys*. *Zool. Listy*, 20: 39-40.

LAVRENCHENKO, L.A., O.P. LIKHNOVA, M.I. BASKEVICH & AFEWORK BEKELE (1998). Systematics and distribution of *Mastomys* (Muridae, Rodentia) from Ethiopia, with the description of a new species. *Z. Säugetierkunde,* 63: 37-51.

LAVRENCHENKO, L.A., A.N MILISHNIKOV, V.M. ANISKIN & A.A. WARSHAVSKY (1999). Systematics and phylogeny of the genus *Stenocephalemys* Frick, 1914 (Rodentia, Muridae): a multidisciplinary approach. *Mammalia,* 64, 475–494.

LECOMPTE, E., L. GRANJON, J.K. PETERHANS & C. DENYS (2002). Cytochrome b-based phylogeny of the *Praomys* group (Rodentia, Murinae): a new African radiation? C*.R. Biologies*, 325: 827-840.

LEE, M.R. & L.K. MARTIN (1980). *Mastomys* (=*Praomys*) *natalensis* is not a *Rattus* (Mammalia: Rodentia): karyological evidence. *Cytogenet. Cell Genet*., 28: 95-103.

LEIRS, H. (1994). Population ecology of *Mastomys natalensis* (Smith, 1834). *Implications for rodent control in Africa*. Belgian administration for Development Cooperation, Agricultural Ed. n° 35, Brussels.

LYONS, N.F., D.H. Gordon & C.A. Green (1980). G-banding chromosome analysis of species A of the *Mastomys natalensis* complex (Smith, 1834) (Rodentia Muridae). *Genetica*, 54: 209-212.

MATTHEY, R. (1954). Nouvelles recherches sur les chromosomes des Muridae. *Caryologia,* 6: 1–44.

MATTHEY, R. (1955). Noveaux documents sur les chromosomes des Muridae. Problemès de cytologie comparée et de taxonomie chez les Microtinae. *Rev. Suisse Zool*., 62 : 163-206.

MATTHEY, R. (1956). La formule chromosomique de quelques Murinae (Muridae-Rodentia-Mammalia). Archiv. der Julius Klaus-Sitftung fur Vererbungsforschung. *Sozialanthr. Rassen.,* 31: 294-306.

MATTHEY, R. (1959). Formules chromosomiques de Muridae et de Spalacidae. La question du polymorphisme chromosomique chez les mammifères. *Rev. Suisse Zool*., 66: 175–209.

MATTHEY, R. (1963). Polymorfisme chromosomique intraspècifique et intraindividuel chez *Acomys minous* Bate (Mammalia-Rodentia-Muridae). *Rev. Suisse Zool*., 72: 119-144.

MATTHEY, R. (1964). Evolution chromosomique et speciation chez les *Mus* du sous-genre *Leggada* Grey 1837. *Experientia*, 20: 1-9.

MATTHEY, R. (1965a). Le problème de la détermination du sexe chez *Acomys selousi* De Winton – Cytogénétique du genre *Acomys* (Rodentia-Murinae). *Rev. Suisse Zool*., 72: 119–144.

MATTHEY, R. (1965b). Etudes de cytogènètique sur des Murinae Africains appartenant aux genres *Arvicanthis*, *Praomys, Acomys* et *Mastomys* (Rodentia). *Mammalia*, 29: 228-249.

MATTHEY, R. (1966a). Cytogénétique et taxonomie des rats appartenant au sous-genre *Mastomys* Thomas (Rodentia – Muridae). *Mammalia*, 30: 105-119.

MATTHEY, R. (1966b). Une inversion péricentrique à l'origine d'un polymorphisme chromosomique non-Robertsonienne dans une population de *Mastomys* (Rodentia – Murinae). *Chromosoma*, 18: 188-200.

MATTHEY, R. (1967). Note sur le cytogénétique de quelques muridés africains. *Mammalia*, 31: 281-287.

MATTHEY, R. (1968) Cytogénétique et Taxonomie du genre *Acomys – A. percivali* Dollmann et *A. wilsoni* Thomas, espèces d'Abyssinie. *Mammalia*, 32: 621–627.

MATTHEY, R. (1969). Chromosomes de Gerbillinae. Genres *Tatera* et *Taterillus*. *Mammalia*, 33: 522-528.

MATTHEY, R. (1971). Dimorphisme sexuel du chromosome X et caryotype de *Grammomys surdaster* Th. et Wrough. (Mammalia: Muridae). *Boll. Zool*., 38: 183-186.

MATTHEY, R. & F. PETTER (1970). Etude cytogénétique et taxonomique de 40 *Tatera* et *Taterillus* provenant de Haute-Volta et de République Centrafricaine (Rongeurs, Gerbillidae). *Mammalia*, 34: 585-597.

MEESTER, J. & H.W. SETZER (1971). *The mammals of Africa, an identification manual*. Smithsonian Institution Press, Washington D.C.

MENAUT, C. (1983). *The vegetation of African savannas*. In: BOULIÈRE, J. (ed), *Ecosystems of the world*. Elsevier, Amsterdam: 109-149.

MISONNE, X. (1969). African and Indo-Australian Muridae: Evolutionary trends. *Ann. Mus. Roy. Afr. Cent*., Tervuren, Serie IN-8, Sci. Zool.: 172: 1-219.

MISONNE, X. (1974). Order Rodentia. Part 6. In: MEESTER J. & H.W. SETZER (eds), *The mammals of Africa: and identification manual.* Washington, D.C. Smithsonian Institution Press: 1-39.

MONTGELARD, C., C.A. MATTHEE & TJ. ROBINSON (2003). Molecular systematics of dormice (Rodentia: Gliridae) and the radiation of *Graphiurus* in Africa. *Proc. R. Soc. Lond.*, 270: 1947–1955.

MUSSER, G.G. & M.D. CARLETON (1993). *Family Muridae*. In: WILSON, D.E.& D.H. REEDER (eds), *Mammal species of the world. A taxonomic and geographic reference*. Smithsonian Institute Press, Washington D.C.

MUSSER, G.G. & M.D. CARLETON (2005). Superfamily Muroidea. In: WILSON, D.E. &, D.M. REEDER (eds), *Mammal species of the world: a taxonomic and geographic reference, 3rd edition*. Baltimore: Johns Hopkins University Press.

ORLOV, V.N., N.SH. BULATOVA & A.N. MILISHNIKOV (1989). Karyotypes of some mammalian species (Insectivora, Rodentia) in Ethiopia. In: SOKOLOV V.E. (ed), *Ecological and Faunistic studies in South-Western Ethiopia*. USSR Committee for the UNESCO Programme of Man and Biosphere (MAB) and Institute of Evolutionary Morphology and Animal Ecology of the USSR Academy of Science, Moscow: 72-94 (in Russian).

ORLOV, V.N., M.I. BASCKEVICH & N.SH. BULATOVA (1992). Chromosomal sets of rats of the genus *Arvicanthis* from Ethiopia. *Zool. Zh*., 71: 103-112.

PAVLINOV, I.J. (1999). Current concepts of Gerbillid phylogeny and classification. In: DENYS, C., L. GRANJON & A. POULET (eds), *African Small Mammals*. Proceedings of the 8th Inter-

national Symposium on African Small Mammals. IRD Editions, Paris: 141–149.

PHILIPPI, T. (1994). Zur innerartlichhen Variabilität von *Arvicanthis niloticus* Desmarest 1822 in Ägypten und im Sudan (Mammalia: Rodentia: Muridae). *Sencken. biol*., 73: 39-44.

QUMSIYEH, M.B. (1986). Phylogenetic studies of the rodent family Gerbillidae: chromosomal evolution in the southern African complex. *J. Mamm*., 67: 680–692.

QUMSIYEH, M.B., M.J. HAMILTON & D.A. SCHLITTER (1987). Problems in using Robertsonian rearrangements in determining monophyly: example from the genera *Tatera* and *Gerbillurus*. *Cytogenet. Cell Genet*., 44: 198–208.

QUMSIYEH, M.B., S.W. KING, J. ARROYO-CABRALES, I.R. AGGUNDEY, D.A. SCHLITTER, R.J. BAKER & K.J. MORROW JR. (1990). Chromosomal and protein evolution in morphologically similar species of *Praomys* sensu lato (Rodentia, Muridae). *J. Hered.,* 81: 58-65.

ROCHE, J., E. CAPANNA, M.V. CIVITELLI & A. CERASO (1984). Caryotypes des rongeurs de Somalie. 4. Premiere capture de rongeurs arboricoles du sous-genre Grammomys (genre Thamnomys, murides) en Republique de Somalie. *Mon. Zool. It.*, 19: 259-277.

RUSSO, I.M., C.T. CHIMIMBA & P. BLOOMER (2001). Geographic mtDNA variation in *Aethomys namaquensis* (Rodentia: Muridae). Proceedings of 8th International Theriological Congress, sun City, South Africa, 12-17 August, 2001.

SCHLITTER, D.A., L.W. ROBBINS & S.L. WILLIAMS (1985). Taxonomic status of dormice (genus *Graphiurus*) from west and central Africa. *Ann. Carn. Mus*., 54: 1-9.

SINGLETON, G.R., L.A. HINDS, H. LEIRS & Z. ZHANG (1999). *Ecologically-based management of rodent pest.* ACIAR Monograph No. 59, Canberra.

STAPLERAT, (2003). *Protecting staple crops in eastern Africa: integrated approaches for ecologically based field rodent pest management*. Final report. Contract Number ICA4-CT-2000-30029, an European Union Shared-Cost Project.

STITOU, S., M. BURGOS, F. ZURITA, R. JIMENEZ, A. SANCHEZ & R. DIAZ DE LA GUARDIA (1997). Recent evolution of NOR-bearing and sex chromosomes of the North African rodent *Lemniscomys barbarus*. *Chromosome Res*., 5: 481–485.

TRANIER, M. (1974). Parenté des *Mastomys* du Maroc e du Sénégal (Rongeurs, Muridés). *Mammalia*, 38: 558-560.

TRANIER, M. & H. DOSSO (1979). Recherches caryotypiques sur les rongeurs de Cote d'Ivoire: résultats préliminaires pour les milieux fermés. *Mammalia,* 43: 254-256.

TRANIER, M. & J.C. GAUTUN (1979). Recherches caryologiques sur les rongeurs de Cote d'Ivoire: resultats preliminaires pour le milieu ouvert. Le cas d'*Oenomys hypoxanthus ornatus*. *Mammalia,* 43: 252–254.

VAN DER STRAETEN, E. & W.N. VERHEYEN (1978). Karyological and morphological comparison of *Lemniscomys striatus* (Linnaeus, 1758) and *Lemniscomys bellieri* Van der Straeten, 1975, from Ivory Coast (Mammalia, Muridae). *Bull. Carnegie Mus. Nat. Hist.*, 6: 41–47.

VAN DER STRAETEN, E. & W.N. VERHEYEN (1980). Relations biomètriques dans le groupe spécifique *Lemniscomys striatus* Mammalia, Muridae). *Mammalia*, 44: 73–82.

VAN DER STRAETEN, E. & W.N. VERHEYEN (1985). Premiere capture de *Lemniscomys striatus* au Burkina-Faso. *Mammalia*, 49: 576–577.

VERHEYEN, E., M. DILLEN, C. FADDA, M. COLYN, L.S. MULUNGU, N.O. OGUGE, J. KERBIS & W. VERHEYEN (2003). The phylogeny and identification of African thicket rat species (Muridae, *Grammomys, Thamnomys*) based on 16S mtDNA sequences. African Small Mammals, 9th International Symposium, Morogoro, Tanzania, 14-18 July: 76.

VEYRUNES, F., J. CATALAN, B. SICARD, T.J. ROBINSON, J.M. DUPLANTIER, L. GRANJON, G. DOBIGNY & J. BRITTON-DAVIDIAN (2004). Autosome and sex chromosome diversity among the African pygmy mice, subgenus *Nannomys* (Muridae; *Mus*). *Chromosome Res*., 12: 369–382.

VEYRUNES, F., J. BRITTON-DAVIDIAN, T.J. ROBINSON, E. CALVET, C. DENYS & P. CHEVRET (2005). Molecular phylogeny of the African pygmy mice, subgenus Nannomys (Rodentia, Murinae, Mus): Implications for chromosomal evolution. *Mol Phylogenet. Evol*., 36: 358-369.

VIEGAS-PÉQUIGNOT, E., M. RICOUL, F. PETTER & B. DUTRILLAUX (1987). Cytogenetic study of three forms of *Mastomys* (Rodentia, Muridae). *Bras. J. Genet*., 10: 221-228.

VISSER, D.S. & T.J. ROBINSON (1986). Cytosystematics of the South African *Aethomys* (Rodentia: Muridae*). S. Afr. J. Zool*., 21: 264-68.

VOLOBOUEV, V., E. VIEGAS-PÉQUIGNOT, F. PETTER & B. DUTRILLAUX (1987). Karyotypic diversity and taxonomic problems in the genus *Arvicanthis. Genetica,* 72: 147-150.

VOLOBOUEV, V., E. VIEGAS-PÉQUIGNOT, M. LOMBARD, F. PETTER, J.M. DUPLANTIER & B. DUTRILLAUX (1988). Chromosomal evidence for a polytypic structure of *Arvicanthis niloticus* (Rodentia, Muridae). *J. Zool. Syst. Evol. Res*., 26: 276-285.

VOLOBOUEV, V.T., M. TRANIER & B. DUTRILLAUX (1991). Chromosome evolution in the genus *Acomys* (Rodentia, Muridae): chromosome banding analysis of *Acomys* cf. *dimidiatus. Bonn. Zool. Beitr.*, 42: 253-260.

VOLOBOUEV, V.T., J.-C. GAUTUN & M. TRANIER (1996). Chromosome evolution in the genus *Acomys* (Rodentia, Muridae): chromosome banding analysis of *Acomys cahirinus. Mammalia*, 60: 217-222.

VOLOBOUEV, V.T., A. HOFFMANN, B. SICARD & L. GRANJON (2001). Polymorphism and polytypy for pericentric inversions in 38-chromsomae *Mastomys* (Rodentia, Murinae) and possible taxonomic implications. *Cytogenet. Cell Genet*., 92: 237-242.

VOLOBOUEV, V.T., J.-F. DUCROZ, V.M. ANISKIN, J. BRITTON-DAVIDIAN, R. CASTIGLIA, G. DOBIGNY, L. GRANJON, M. LOMBARD, M. CORTI, B., SICARD & E. CAPANNA (2002a). Chromosomal characterization of *Arvicanthis* species (Rodentia, Murinae) from western and central Africa: Implications for taxonomy. *Cytogenet. Gen. Res.,* 96: 250–260.

VOLOBOUEV, V.T., V.M. ANISKIN, E. LECOMPTE & J.-F. DUCROZ (2002b). Patterns of karyotype evolution in complexes of sibling species within three genera of African muroid rodents inferred from comparison of cytogenetic and molecular data. *Cytogenet. Gen. Res*., 96: 261-275.

WAHRMAN, J. & A. ZAHAVI (1953). Intra-generic differences in chromosome numbers of spiny-mice (Rodentia, Murinae). *Bull. Res. Council Israel*, 3: 265

WHITE, F. (1986). *La vegetation de l'Afrique*. UNESCO, Paris.

YALDEN, D.W., M.J. LARGEN & D. KOCK (1976). Catalogue of the mammals of Ethiopia. 2. Insectivora and Rodentia. *Mon. Zool. It., suppl*., 8: 1-118.

ZIMA, J., M. MACHOLÁN & M.G. FILIPPUCCI (1994). Chromosomal variation and systematics of Myoxids. *Hystrix,* 6: 63-76.