Unterarten aus den Niederlanden und Holstein bzw. aus Holstein und Polen: Bei *domesticus* führten die Angriffe dominanter Männchen häufiger zum Tode der unterlegenen Männchen als bei *musculus*. In Konfrontationen zwischen Männchen der verschiedenen Unterarten siegten immer die (schwereren) *domesticus*-Tiere. Ihre Überlegenheit könnte die Verschiebung der Unterartgrenze nach Osten erklären.

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The African rodent *Colomys goslingi* Thomas and Wroughton, 1907 (Rodentia: Muridae) – a predator in limnetic ecosystems

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Abstract

The African rodent *Colomys goslingi* (Muridae) nearly always lives close to running waters. In this study the feeding biology of this species, based mainly on the morphology of the intestinal tract, on stomach contents, and on observation of its preying behaviour is investigated.

Evidently *Colomys* is a predator in limnetic ecosystems, as running water invertebrates heavily predominate in the stomach contents. In the laboratory *Colomys* also fed on vertebrates (fishes, tadpoles), which were actively hunted. High sensory performances of *Colomys* can be expected in

conjunction with the different patterns of preying behaviour, which in the natural habitat is assumed to occur in three modes: passive filter feeding, active hunting, and active collecting.

The feeding biology of *Colomys goslingi* as a whole is not comparable to any other known within the rodents.

Introduction

Rodents are usually roughly classified as "vegetarians", although a relatively large percentage of the species and the genera feeds on both, plant and animal material, and some species are truely omnivorous. However, truely carnivorous species, which ingest more than 50 % or even 80 % animal food, are very rare.

Of the African rodents only few representatives of the families Cricetidae and Muridae can be classified as mainly or exclusively carnivorous. Within the Cricetidae the Dendromurine *Deomys ferrugineus* feeds between 80–100 % on insects (DIETERLEN 1976b). The rare species *Leimacomys büttneri* – also a member of the Dendromurinae – seem to feed on material comparable to the food of *Deomys* (DIETERLEN 1976b). Within the family Muridae carnivorous feeding is known for species of the genera *Zelotomys* (MISONNE 1965) and *Lophuromys* (DIETERLEN 1976a). Eight of the nine known species of the latter genus feed between 50–100 % on insects. A further representative of the Muridae, the monospecific *Colomys goslingi*, is generally known as a predator near or in forest brooks, a peculiar feeding habit in the family. However, details on the composition of the food as well as on the feeding behaviour of this species are completely unknown.

These details are of special interest, because the preying behaviour of this nocturnal murid in running water could be expected to require a highly developed sense of orientation. The high turbulence of natural running waters probably makes the hunt for its prey more difficult. Moreover, the current presents a certain risk of accident, particularly for small animals. These topics were the main reasons for this study. In addition, investigations on the relationship between higher vertebrates and limnetic ecosystems are of more general interest, as such researches have rarely been done up to now. The main concern with rodents has been the influence of their building activities on the structure of inland waters (cf. HYNES 1972), whilst the predation of species of this order of mammals has hardly been mentioned in the limnologic literature.

Therefore this paper deals exclusively with the feeding biology of *Colomys goslingi*. A further publication will deal more comprehensively with the systematics, ecology, and biology of this species and will sum up the adaptions in morphology and feeding biology of rodents living near or in inland waters.

Short characterization of *Colomys goslingi*

Colomys goslingi can be easily identified by the colouration of its dense woolly coat, which is unique within African Muridae. The upper side is brown-gray with red or black shades, the ventral side is purely white. The mean values of some important characteristic measurements of the body of the adult animal are as follows: length of the head and body 125 mm, length of the tail 160 mm, length of the hind foot 37–38 mm, weight 55–60 g. The unusual long hind foot, which amounts to about 30 % of the length of the head and body, is one conspicuous fact. Other striking characteristics are the shape of the mouth region and the arrangement of the extremely long vibrissae (cf. Fig. 2). Further characteristics will be published elsewhere.

The distributional area of *Colomys* is roughly restricted to the central African forest region and its branches. Evidence of *Colomys* is concentrated in the East and Northeast of the Zaire. It is not clear in the moment, whether *Colomys* is evenly distributed over the whole African forest region or not. A clear patchy distribution is known from North Zambia, East Africa, and Ethiopia. Evidence for the Southern Sudan is quite new (DIETERLEN and RUPP 1979). Due to the fact that *Colomys* is restricted to running waters in (mainly) primary forest and its abundance in such areas is quite low the species is regarded as being a rare one. Thus, only 150–200 specimens are in the collections of the museums of the world.

Material and methods

A total of 55 specimens of *Colomys* was captured with snap traps (using, in most cases, peanuts as bait) by DIETERLEN in Zaire and Rwanda and by RUPP and NIKOLAUS in Southern Sudan. The period between the trapping and the removal of the dead specimens from the traps was between 2 and 12 hours.

A subsample of 21 specimens was investigated with regard to the length relations of different structures in the digestive tract and/or a rough classification of the stomach contents immediately after removal from the traps. After cutting the mesentery the whole intestinal tract was stretched on a cardboard, eventually fixed by a needle, and the single parts, small intestine, coecum, and colon were measured in this position. For investigation of stomach contents the stomachs were opened and the food was transferred into glasses with alcohol (ca. 70 %), in which the material was stored until further examination in the laboratory. The 21 specimens further investigated in this study are briefly characterized in Table 1. It is important to note that the specimens, from which the stomach contents were studied, belonged to four different groups: all specimens with a K in front of the collection number came from brooks in the mountain region (Parc National du Kahuzi-Biega = PNKB). The only exception: K 2799 was captured at the edge of a swamp. All specimens with an I in front of the collection number came from brooks in the lowland region (Irangi), and a single specimen (N 1385) was trapped in the Southern Sudan. A detailed description of all trapping areas will be given by DIETERLEN (in preparation).

Table 1

Specimens of *Colomys goslingi* examined in this study

Number in collection	Sex	Weight	Date of collection	Place of collection
K 1298[+]	♂	54 g	21/ 1/72	Tshibinda/PNKB
K 2427[+]	♀	52 g	13/10/72	Lemera-Nyabuhuga/PNKB
K 2469[+]	♀	64 g	9/11/72	Lemera-Nyabuhuga/PNKB
K 2470[+]	♀	65 g	9/11/72	Lemera-Nyabuhuga/PNKB
K 2471[+]	♂	57 g	9/11/72	Lemera-Nyabuhuga/PNKB
K 2624[+]	♀	52 g	14/ 2/73	Lemera-Nyabuhuga/PNKB
K 2799[+]	♂	55 g	12/10/74	Mukaba/PNKB
K 2929[+]	♂	64 g	20/10/74	Mt. Kahuzi/PNKB
I 366[+]	♂	62 g	13/10/71	Irangi/East Zaire
I 543[+]	♂	50 g	5/ 1/72	Irangi/East Zaire
I 545[+]	♀	59 g	6/ 1/72	Irangi/East Zaire
I 736[+]	♀	52 g	22/ 3/72	Irangi/East Zaire
I 750[+]	♂	50 g	23/ 3/72	Irangi/East Zaire
I 1173[+]	♀	46 g	16/ 8/72	Irangi/East Zaire
I 1724	♀	60 g	27/ 2/73	Irangi/East Zaire
N 1385[+]	–	–	28/ 1/79	Gilo/Imatong Mts/Sudan
D 3448	♀	52 g	20/ 8/64	Uinka/Rwanda
D 3450	♂	60 g	21/ 8/64	Uinka/Rwanda
D 3451	♂	38 g	21/ 8/64	Uinka/Rwanda
D 3497	♂	42 g	27/ 8/64	Uinka/Rwanda
D 3515	♀	64 g	2/ 9/64	Uinka/Rwanda

[+] = stomach content investigated; PNKB = Parc National du Kahuzi-Biega, Zaire.

In the more detailed analysis of the food the larger particles in the stomach contents were sorted out with the help of a stereomicroscope[1]. Afterwards the remaining fine food mash was transferred into aqueous potassium hydroxide and boiled until the liquid became clear. From this liquid single chitinous parts could be sorted out, which were important for the determination of the prey.

As the captured *Colomys* stayed in the traps for different periods (cf. above), their stomach contents were more or less digested. Moreover, the compact structures of the prey were more or less broken down. The degree of disintegration obviously depends on the kind and size of the prey as well as on the different chewing intensities of the single *Colomys* specimens. Thus the difficulty in

[1] This material is stored in the collection of the Staatliches Museum für Naturkunde in Stuttgart.

determining the organisms depended on the condition of the stomach content. In addition, the level reached in the determination depends, particularly if a more or less crushed food mash from a tropical predator is considered, on the experience and the collection of intact food organisms of the investigator (ST.). Both decrease in the following order: Hydropsychidae – Trichoptera – limnetic invertebrates – terrestrial invertebrates – vertebrates – plants. While a caddisfly was probably able to be determined to the generic level with the help of a single chitinous part, this was not possible e. g. in terrestrial spiders, from which a part of the eye-rows or a part of the spinning mammilla was found and the determination ended at the level of Araneae.

All these factors were a handicap during the analysis, especially if quantitative aspects of the food items are considered – a field that is well described methodically in fish studies (cf. WINDELL 1971). Thus the quantitative treatment of the stomach contents is mainly justified by the unique material under study and the fact that the more detailed determination of the limnetic food items will allow conclusions about the preying behaviour of Colomys in natural running waters.

The observations of the feeding behaviour in the laboratory (D.) are based on one adult male, which was trapped on 8th Aug. 1972 near a brook in the primary forest of Lemera/PNKB. This male was caught in the trap by its right hind foot, which was slightly hurt. The foot remained crippled. However, the crippled foot did not hinder the animal's movement or preying behaviour. After transport to Germany the male lived from the 11th Aug. 72 until its death on 17th Febr. 75 in a plastic terrarium, 100 × 60 × 60 cm. In the terrarium it inhabited a small burrow made from pressed peat mold. A plastic basin 40 × 30 cm was placed in its living space and it was always filled with fresh water, usually up to a height of 3–4 cm. All observations on the feeding behaviour were carried out in this terrarium. As Colomys is nocturnal, this was done with the help of a weak light, which obviously did not affect the animal's behaviour.

The male was usually fed with dead shrimps (Crangon crangon), live prey, such as Oligochaeta, tadpoles, of fishes (cf. below) was offered occasionally.

Feeding biology of Colomys goslingi

The aim of this chapter is to describe all known facts relating to the feeding biology of Colomys, i. e. besides results on the preying behaviour and the stomach contents, morphological and ecological details of Colomys will also be presented.

Morphology of the intestinal tract

It is a well accepted rule that the length of the intestinal tract in relation to the body length as well as the relation of the length of the different compartments of the intestinal tract relative to each other is different in carnivorous and herbivorous mammals. This is also confirmed in some African Muridae by DIETERLEN (1967).

The length of the intestinal tract of Colomys only amounts to 5,8-times the head and body length – a low value, typical for carnivorous Muridae.

The length of different parts of the intestinal tract is given in Table 2. The length of the whole intestinal tract of Colomys is relatively short compared to that of herbi- or omnivorous rodents and the relative lengths of the coecum and the large intestine are also short. The relative length of the different parts of the intestinal tract is comparable to that of Lophuromys (cf. Table 2). The latter genus is well known to feed mainly on animal food items (DIETERLEN 1976a).

Remarks on the natural habitat and the preying behaviour in the field

Nearly all specimens of Colomys from East Zaire and Rwanda captured by one of us (D.) came from the immediate vicinity of freshwaters. Although trap lines were set up in all biotopes in a lot of different forest regions, most of the trapped Colomys were caught not further than 5 m from running waters. The same was observed by RUPP and NIKOLAUS (pers. comm.), who captured numerous specimens in the Sudan (Imatong Mts. and the region south of Yei), by KINGDON (1974) in the Bwamba forest in Uganda, and by EISENTRAUT (1975) in West Cameroon. Trapped Colomys are very rarely reported from

Table 2

Relations in the intestinal tract of *Colomys goslingi* compared to that of well known carnivorous Muridae, *Lophuromys* spp.

(Data on the latter from DIETERLEN 1976a)

Number in collection	Head and body	Length (in mm) of Small intestine	Coecum	Large intestine	Total intestine
K 2427	105	510	25	70	605
K 2469	130	570	30	80	680
K 2470	126	600	30	80	710
K 2471	120	540	35	90	665
K 2624	115	460	20	70	550
I 1173	115	500	25	70	595
I 1724	120	620	25	80	725
D 3448	112	610	30	80	720
D 3450	117	690	30	95	815
D 3451	103	560	25	80	665
D 3497	107	560	30	75	665
D 3515	121	790	30	100	930
Mean:	116	584	26	81	691
Range:	103–130	460–790	20–35	70–100	550–930
Relative length of the single parts of the intestinal tract		84,5 %	3,8 %	11,7 %	
The same in *Lophuromys*		77 %	7 %	16 %	

swamps or the edges of swamps (MISONNE 1963). The material studied here contains only one specimen trapped at the edge of a swamp (Mukaba/PNKB), at a distance of about 100 m from an outflowing brook. Although *Colomys* is closely linked to the above mentioned freshwater biotopes, it was occasionally observed in the houses of humans near the courses of streams, where it fed on stored provisions (KINGDON, 1974; NIKOLAUS pers. comm.).

The preying behaviour of *Colomys* in the field was observed and uniquely described by KINGDON (1974):

"I have watched *Colomys* searching for food in watery mud; the animal wades through the water raising itself as high as it can on its toes. While the forelegs are occupied sifting mud and debris, the hindlegs are sometimes placed very wide apart to achieve balance. The nose is held close to the water's surface with the vibrissae spread out so that they are in contact with the water: presumably they assist in the detection of prey disturbed by the sifting hands. A quick pounce marks a capture and the prey may then be taken to a drier spot. When the object is a worm, the rat works it vigorously through the hands pushing the body contents down the length of the worm as it swallows the head first. The animals's whiskers are the object of constant grooming and there can be little doubt that the peculiar muzzle and vibrissae are an important specialization . . .".

The diet in the natural habitat

All the 15 somaches studied contained macroinvertebrates (Table 3). Fairly intact plant material (?seeds, ?buds, fragments of leaves) were found in only two stomaches. Moreover, nearly every stomach contained small amounts of detritus material, which is assumed to come from the intestinal tracts of the preyed macroinvertebrates, for several of the prey taxa are known to be detritivorous.

Obviously the information on the food items based on the stomach contents greatly depends on the degree of digestion of the food mash. Thus, quantitative aspects must be considered with caution.

Table 3

Stomach contents of *Colomys goslingi*

The specimens of *Colomys* are grouped according to the regions, the sexes, and within the sexes from left to right in order of decreasing weight. The food items are grouped according to the habitat in which they were usually found

Degree of digestion	Near brooks in PNKB ♂♂			Near brooks in PNKB ♀♀				Swamp Mukaba, PNKB ♂	Irangi ♂♂		Irangi ♀♀				Gilo, Im. Mts
	K2671 high	K2929 high	K1298 low	K2470 high	K2469 high	K2427 low	K2624 low	K2799 medi	1366 medi	1543 high	1750 low	1545 high	1736 medi	11173 high	N1385 high
C: Psephenidae (l)											1				
T: Cheumatopsyche (l)				2	1				1			1			
T: Hydropsyche (P)										1			1		
T: Leptonema (l)			2	1	4	1									
T: Macronema (l)						1	9				13		2		
T: Thylakion (l)						1									
T: Philopotamidae (l)											1				
D: Simuliidae (l)						1									
C: Elmidae (l)	1										1	1			
E: Baetidae (l)				1							1	1			1
L: Pyralidae (l)						1									
D: Rhagionidae s.l. (l)						1									
T: Goerodes (P)								4							
T: Goerodes (l)		2	24			34		47							
T: Lepidostomatidae (P)		3					?7	1							
T: Lepidostomatidae (l)										1					
P: Neoperla (l)		1	1	2											
E: Heptageniidae (l)	1		2	1											
T: Leptoceridae (l)	2		1								2			1	
T: Polycentropodidae (P)						?1									?4
T: Polycentropodidae (l)						?3									?4
D: Chironomidae (l)															1
E: Leptophlebiidae (l)															?4

Habitat groupings (right margin): *almost lotic* — *limnetic* — *lotic and/or lentic*

Food items	almost lentic		unknown		terrestric		Total
D: Dixidae (l)		1					1
T: Leptocerina (l)	31						31
O: Libellulidae (l)	2						2
H: Belostomatidae (l)	3		?1				3
H: Veliidae (i)			?1				
Nematomorpha	?1				+		1
T: Hydropsychidae (i)	1	1	1				
D: Tabanidae (l)	2	1	1				
D: Limoniidae (l)	1	1	1	1	+		
insecta indet. (p)	?1	1	1	2	1		
Lepidoptera (l)	?1	1	1	?1			
Coleoptera (i)	1	1	1				
insecta wings (C, D, and indet.)	17	1	1	2	+	+	
Gastropoda	1	1	1	1	+	+	
Araneae	2	1	2	1	+	+	
hairs				+	+		
plant material				+	+		
Arthropoda indet.				+	+		
Total	6	5	34	11	7	48	23 55 23 4 23 5 33 12

PNKB: Parc National du Kahuzi-Biega. ? in front of values: identification uncertain. Large letter in front of the food items indicate insect orders: C: Coleoptera, D: Diptera, E: Ephemeroptera, H: Heteroptera, L: Lepidoptera, O: Odonata, P: Plecoptera, T: Trichoptera, (i): imago, (p): pupa, (l): larva.

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Stomach contents of *Colomys goslingi*

The specimens of *Colomys* are grouped according to the regions, the sexes, and within the sexes from left to right in order of decreasing weight. The food items are grouped according to the habitat in which they were usually found

Degree of digestion	Near brooks in PNKB ♂♂ K2671 high	K2929 high	K1298 low	♀♀ K2470 high	K2469 high	K2427 low	K2624 low	Swamp Mukaba, PNKB ♂ K2799 medi.	Irangi 1366 medi.	♂♂ 1543 high	1750 low	♀♀ 1545 high	1736 medi.	I1173 high	Gilo, Im. Mts N1385 high	Habitat
C: Psephenidae (l)				2	1					1						almost lotic
T: Cheumatopsyche (l)					1											
T: Hydropsyche (p)										1						
T: Hydropsyche (l)										1						
T: Leptonema (p)				1			1									
T: Leptonema (l)		2		4	1	1	9									
T: Macronema (l)											13		2			
T: Thylakion (l)					1											
T: Philopotamidae (l)					1					1						
D: Simuliidae (l)					1											
C: Elmidae (i)			1							1						
C: Elmidae (l)												1			1	
E: Baetidae (l)	1		1	1	1					1		1				
L: Pyralidae (l)						1										
D: Rhagionidae s.l. (l)						1										
T: Goerodes (p)								4								limnetic
T: Goerodes (l)		2	24			1	34	47								lotic and/or lentic
T: Lepidostomatidae (p)							?7									
T: Lepidostomatidae (l)		3	1					1								
P: Neoperla (l)			2	2	1											
E: Heptageniidae (l)	1			1												
T: Leptoceridae (l)	2		1				1			2			1		?4	
T: Polycentropodidae (p)							?1									
T: Polycentropodidae (l)							?3									
D: Chironomidae (l)															1	
E: Leptophlebiidae (l)	1														?4	
D: Dixidae (l)											2				1	almost lentic
T: Leptocerina (l)														31		
O: Libellulidae (l)								3								
H: Belostomatidae (l)													?1			
H: Veliidae (i)															?1	
Nematomorpha						?1										
T: Hydropsychidae (i)			1						?1							unknown
D: Tabanidae (l)					1								?1			
D: Limoniidae (l)									2	1						
insecta indet. (p)			1				1		1							
Lepidoptera (l)					?1					1	1					terrestric
Coleoptera (i)												1				
Coleoptera (l)									17							
insecta wings (C, D, and indet.)				1	1				1			1	2			
Gastropoda				1							1					
Araneae	1					2	1		2	1						
hairs				+												
plant material			+	+												
Arthropoda indet.			+						+					?+	+	
Total	6	5	34	11	7	48	23	55	23	4	23	5	5	33	12	

PNKB: Parc National du Kahuzi-Biega. ? in front of values: identification uncertain. Large letter in front of the food items indicate insect orders: C: Coleoptera, D: Diptera, E: Ephemeroptera, H: Heteroptera, L: Lepidoptera, O: Odonata, P: Plecoptera, T: Trichoptera, (i): imago, (p): pupa, (l): larva.

Most of the food items were doubtless of limnetic origin. A few prey groups cannot be classified according to their origin, as they may live either limnetic or terrestrial (cf. BADCOCK 1953 for the submersal occurrence of imagines of Hydropsychidae), or could not be identified. Material of terrestrial origin also occurred. The latter may be numerous in single stomachs (e. g. I 366), but seems to be of minor importance if all stomachs examined are considered. Gastropods, of which a radula and an operculum were found but no parts of the shells, were classified as terrestrial ones, for truely aquatic snails were not found in the running waters of that region (STATZNER 1975; VIETS and BÖTTGER 1974). This is probably due to the low calcium concentration in the water mentioned by STATZNER (1975).

From the 294 identified specimens in the prey about 85 % were doubtless of limnetic origin, about 3% were of unknown and about 12% were of terrestrial origin (cf. Fig. 1). It remains uncertain whether the food items of unknown and terrestrial origin were captured inside or outside the water. It is a well known fact, that terrestrial invertebrates which have fallen into running waters drift downstream in or on the water (e. g. BAILEY 1966; TOBIAS and THOMAS 1967; THOMAS 1970).
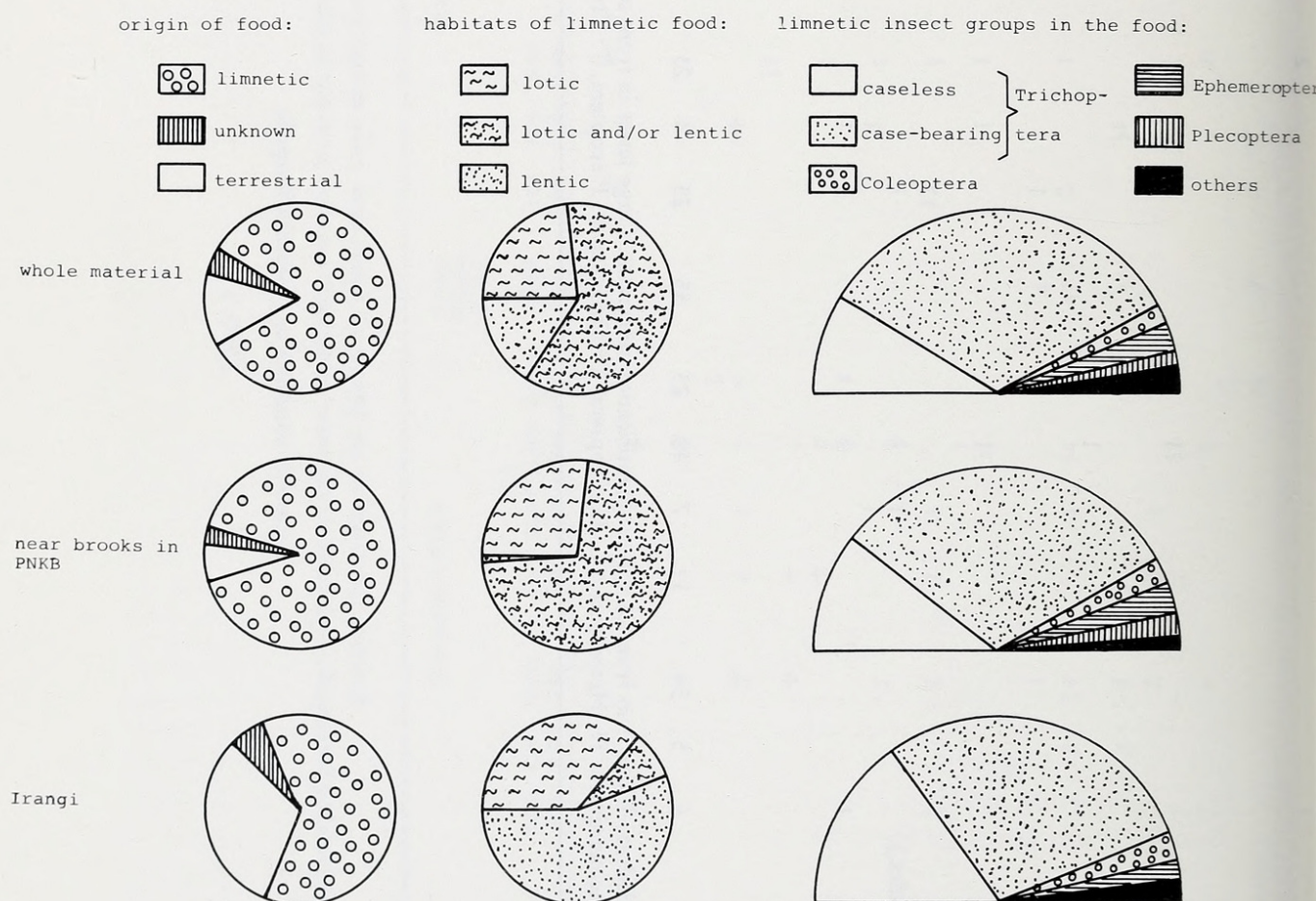

Fig. 1. Proportion (%) of different food items in the stomach contens of Colomys goslingi

Also the classification of the habitats of the limnetic food items cannot prove conclusively that the prey was captured in the habitat mentioned. Migrations are common in the benthic fauna and can occur regularly or occasionally during the development of a species. Besides this, single specimens can usually be found in atypical habitats in any running water. Thus the classification "lotic" (swift flowing water) and "lentic" (still water) are accompanied by an "almost". This almost is further justified by the fact, that some of the

higher taxa also have representative species in other habitats, e. g. in the group of almost lotic food items Baetidae or Elmidae are sometimes found in still waters, i. e. the classification is established mainly for running waters in the Kivu-region (Zaire), based on personal experience (ST.) as on the literature (MARLIER 1954a, b; STATZNER 1973, 1975).

Before going into further details, some points must be briefly discussed: There is no evidence that the sex or the weight of the *Colomys* specimens influenced the stomach contents, although individual differences in the food items occurred. These differences cannot be caused by the fact that the stomaches examined came from specimens captured in all seasons. From a large emergence trap run above a brook in the Kivu-region for 16 months (BÖTTGER 1975; KOPELKE 1978; LEHMANN 1979; STATZNER 1976; ZWICK 1976) we know, that seasonal differences in the emergence of aquatic insects may occur. However, all abundant species studied emerged over the whole year, i. e. larvae must also be present in the aquatic habitat all the year round. Thus the data of Table 3 are roughly comparable, at least if material from the areas PNKB and Irangi is considered.

Table 3 demonstrates that qualitatively all aquatic groups frequently present in lotic and lentic habitats of African running waters occurred in the stomaches of *Colomys*. If the material from the different regions as well as the limnetic food items are treated separately, more details of the feeding biology of *Colomys* become obvious (Table 3, Fig. 1). In Irangi *Colomys* fed more on terrestrial food items than in the Kahuzi-region, which is probably caused by the lower benthic biomass in running waters near Irangi compared to that in the mountain brooks near the Kahuzi (cf. STATZNER 1975; VIETS and BÖTTGER 1974). Differences also exist in the amount of food ingested from lentic and lotic and/or lentic habitats in both regions. However, these differences are mainly due to two food items: *Leptocerina*, a case bearing caddis larva which is able to swim in calm water (MARLIER 1954a) was ingested in great quantities by one specimen of *Colomys* in Irangi, and *Goerodes*, which is assumed to be more abundant in the mountain region (cf. STATZNER 1975), was frequently preyed on in the brooks in the PNKB. Also the *Colomys* captured near the swamp of Mukaba contained numerous larvae of that caddis fly, probably because a running water was situated near the trapping points (cf. above). The genus *Goerodes* is known only from running waters (MARLIER 1962). The differences in the food items ingested between the PNKB and Irangi were to some extent caused by further changes in the benthic fauna, which exhibited a normally occurring altitudinal zonation in that region (STATZNER 1975). However, the classification of the prey according to the limnetic insect groups (Fig. 1) indicates, that the stomach contents reflect more than only the fauna present in the habitats of *Colomys*. If one compares this data with that of the percentage distribution of the fauna in benthic (STATZNER 1975; VIETS and BÖTTGER 1974) or emergence (BÖTTGER 1975) samples of that region, it becomes evident that *Colomys* fed highly selectively. Caddis flies, especially case-bearing ones, are heavily over-represented, whilst Diptera especially are highly under-represented in the stomach contents. This may be related to the size of that prey. However, the smallest animals found in the stomaches were from the Leptoceridae (length: 3 mm) and the Chironomidae (length: 2 mm), i. e. from the case-bearing caddis flies and the Diptera. Thus the difference in size is assumed to be not the only factor leading to the above mentioned differences, a fact we will come back to later in the discussion.

Another topic that will be discussed later is that *Colomys* fed also on pupae of Trichoptera. Before the pupal molt the caddis larvae attach themselves to stones, branches, etc., i. e. if such food items occur in the stomaches, they probably are removed by *Colomys* from the natural substratum. E. g. *Leptonema* or *Macronema* construct pupal cases with larger gravel, which are fixed in places with a fast flowing current. The removal of those pupal cases must be assumed to be quite difficult for any small predator. Unfortunately, *Colomys* never ingested the cases of caddis flies, i. e. the pupal stage was identified with the help of parts of the pupae itselves and not with parts of pupal cases. As the "pharate

imago" (i. e. the free moving stage before the imaginal ecdysis) of caddis flies as well as the pupal exuvia, which may remain in the water after emergence, can be found in the drift (i. e. the free flowing water), we tried to differentiate between the three stages of pupal material, i. e. pupa from the pupal chamber – pharate imago – pupal exuvia. This was not so easy, as parts of the genitalia or wings of the pupa or the old larval exuvia from the pupal chamber, which can be used for the above mentioned classification, were probably overlooked in the food mash. From this examination the following resulted: *Leptonema*-"pupae" were probably pharate imagines, whilst the "pupa" of *Hydropsyche* was an exuvia and the "pupae" of Lepidostomatidae (incl. *Goerodes*) belonged most probably to all three categories, i. e. pupae picked up from the substratum as well as pharate imagines and pupal exuviae, both from the free flowing water, were preyed on.

Observations on the preying behaviour in captivity

As mentioned above, the male *Colomys* observed in captivity was usually fed with shrimps. Terrestrial snails with houses were rejected by that *Colomys*. Of the plant material offered only sunflower seeds were regularly eaten, sometimes also cooked potatoes. Grain, apples, or different vegetables were repeatedly offered, but were all rejected or used in the construction of the burrow.

After nightfall the animal left the burrow, not timidly but with some caution, ran around and then entered the plastic basin, which was filled with water and gravel, without hesitation. If the water was deeper than 4–5 cm it raised itself as high as it could on its toes, as described by KINGDON (cf. above). Shallower water was clearly preferred. Deep water, which forced the animal to swim, was rarely entered voluntarily, not even if food could be found at such places.

As described by KINGDON (1974) *Colomys* moved around with its vibrissae dipped up to half their length in the water while hunting. It persistently sat at the edge of the basin and held the vibrissae into the water (Fig. 2). *Colomys* remained in this position up to several minutes. This behaviour was shown even when no living prey agitated the water surface or no dead food was offered in the water. This resting behaviour was interrupted by short exkursions into the shallow water or another, peculiar behaviour, which cannot be interpreted with certainty up till now: it immersed its head up to the eyes into the water and moved its mouth e.g. 5–6-times up and down – this behaviour was often observed and can probably be interpreted as drinking. However, it is difficult to understand, why the head must be immersed so deeply into the water in order to drink.

This male *Colomys*, which was only fed with dead shrimps and occasionally with live Oligochaeta during the first months in captivity, was offered 16 living tadpoles for the first time in May 1973. The tadpoles were put into the plastic basin, which contained water of about 2 cm deep. The next morning all the tadpoles had disappeared. A few days later approximately the same number of tadpoles (length: 15–20 mm) were offered in the basin. In a weak illumination it could be observed, that *Colomys*
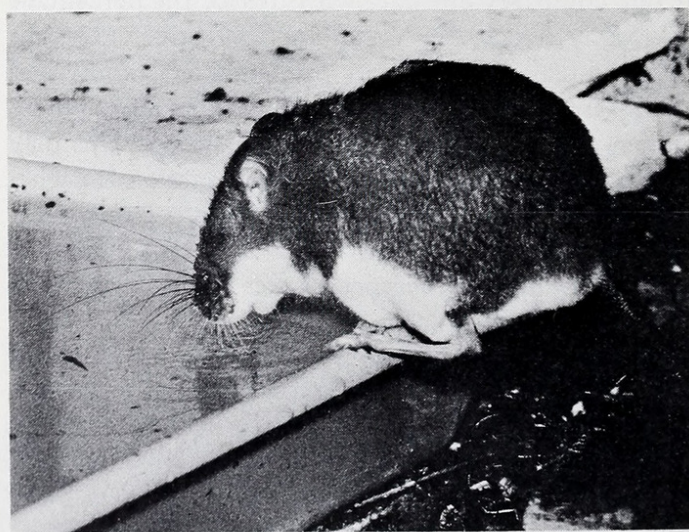
Fig. 2. Colomys goslingi, resting at the edge of the water. The vibrissae are dipped into the water

immediately entered the water and ran around, searching for the prey (Fig. 3a). With fast pendulum movements of the head, which were obviously induced by the tactile response of the vibrissae, *Colomys* followed the tadpoles, which dispersed in the basin. After 3 seconds *Colomys* had captured the first tadpole, which was immediately eaten (Fig. 3b). All this happened so quickly, that the *Colomys* hat eaten 5 tadpoles within about 1 minute, during which it hunted, ate, and rested. Based on these observations it is assumed that the sense of vision is unimportant for the preying behaviour. The only sense organs used in detecting the prey seemed to be the vibrissae, particularly the numerous short ones situated around the mouth.

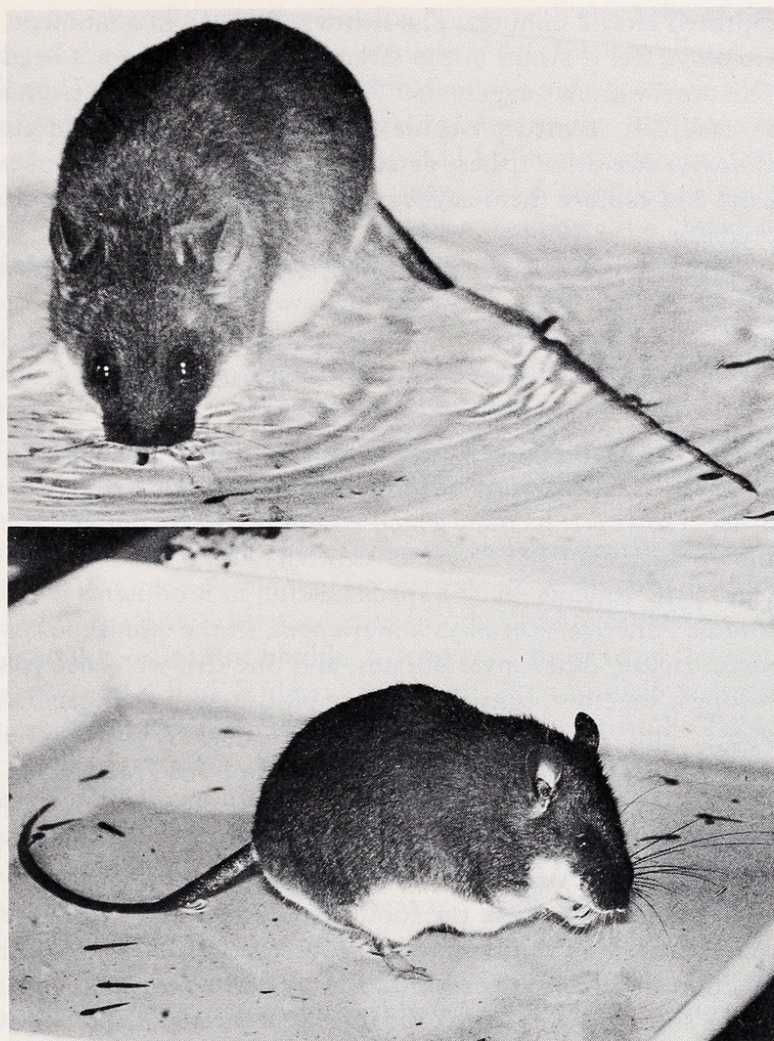Two months later 14 guppies (*Lebistes reticulatus*) were offered in

Fig. 3. *Colomys goslingi*, preying on tadpoles and fishes. – a: Searching for tadpoles in shallow water, the vibrissae are dipped into the water; b: Feeding on a tadpole

the large basin. Probably due to the deep water these guppies did not interest *Colomys* at first. However, all guppies hat disappeared by the next morning. Some weeks later 2 guppies, a male and a female, were put into the basin, where the water was 3–4 cm deep. Immediately after the fishes had been put into the water, *Colomys* left its burrow and quickly investigated the terrarium, which had been cleaned before. Then it entered into the basin and few seconds later it noticed the fishes. Immediately it put the head into the water and followed the fishes as fast as possible, changing direction as jerkily as the fishes. If *Colomys* lost the fish out of its tactile sense, which occurred if a fish was more than 8–10 cm away, it raised its head out of the water and rested for few seconds. Then it started hunting again.

Just as it lost the fishes, if they were a longer distance away, it seemed to get tactile stimulus, if it approached a fish up to 8–10 cm. As this distance is longer than the vibrissae are, which reach a maximum length of 5 cm, *Colomys* must be able to detect something sent out by the fishes.

In contrast to the tadpoles, the guppies tried to escape quickly and *Colomys* lost one or the other of the fishes between 10–20-times, always starting the hunt again after a short rest period (cf. above). After about 3 minutes the smaller fish, the female, was captured by *Colomys*. *Colomys* ate that fish, beginning with the head, at the edge of the basin. Immediately after it had finished its meal it started to hunt the second guppy, which was

captured after 2 minutes. The fish was trapped in a moment, when it tried to pass near the
Colomys, i.e. it swam in the direction of its predator's head, approaching from the front.
The observations suggest that fishes swimming away from the Colomys cannot be caught
so easily. It seemed probable that this behaviour could also be used in the field. There
Colomys can drive fishes, detected in the shallow water of a brook, in the direction of the
bank and capture them at the moment when the fishes try to escape swimming towards the
predator.

That second fish was also eaten, again Colomys started with the head of the fish.

Discussion

Obviously Colomys goslingi is a carnivorous rodent, which only occasionally feeds plant
material. As mentioned in the introduction, this behaviour is not unique in this mammal
order. However, its diet, which is largely based on limnetic macroinvertebrates and, as was
shown in the observations in captivity, even on limnetic vertebrates, is almost unique
within the rodents. Such a specialization in food items is only known from a species from
Middle America, Rheomys underwoodi. In the stomachs of that species a large amount of
insect larvae, other invertebrates, and one fish were also found (HOOPER 1968). Rheomys
belongs, together with the also tropical new-world genera Ichthyomys, Anotomys, Dap-
tomys, and Neustictomys, to the so-called Ichthyomys-group of the Hesperomyinae
(Cricetidae). In its morphology and its diet this Ichthyomys-group is more or less adapted
to the life in or near water (cf. STARRETT and FISLER 1970). Another group of rodents with
differently developed adaptions to aquatic life are the Hydromyinae (Muridae), with a
distribution in Australia, New Guinea, and the Philippines.

Within the Muridae the food items ingested by Colomys are highly specialized and no
representative of this family with comparable food items is known. In addition this isolated
position of Colomys is emphasized by some morphological facts.

As shown in this study, the intestinal tract is adapted to carnivorous feeding in a typical
way. Furthermore the area of the muzzle where the vibrissae are inserted is different from
all known Muridae and also the volume of the brain case is larger when compared with that
of terrestrial Muridae of similar body weight (STEPHAN, pers. comm.).

These two latter facts, in particular, are assumed to be related to the preying behaviour
of this species, as will be discussed in detail later.

Generally the morphological adaptions of Colomys to life in water are relatively poorly
developed, as far as the shape of the ears and the tail are concerned. And indeed the field
observations of KINGDON (1974) and those made in the laboratory investigation described
above suggest that Colomys tries to avoid deeper water and prefers more shallow water,
which is probably caused by the close relation of Colomys to running waters. Swimming in
deep water of e.g. a mountain brook presents the risk of being thrown against a stone etc.

In spite of the poor adaptions to aquatic life in the outer morphology, Colomys feeds on
limnetic food items to a large extent, and probably both, the long, dense, and uniquely
inserted vibrissae and the unique relative volume of the brain allow this species, to be a
little bit "afraid of water" although limnetic food items are preferred.

How is that possible? The curious behaviour of Colomys in dipping its vibrissae into the
water while resting at its edge suggests that the animal captures its food by passive filtration
of the organic drift in such a position. The organic drift is a phenomenon occurring in all
natural running water (cf. reviews of BOURNAUD and THIBAULT 1973; MÜLLER 1974;
WATERS 1972), and detached benthic macroinvertebrates are transported downstream in
the drift in the free flowing water. Terrestrial invertebrates also drift downstream on the
surface of the water. In general, the drift densities are higher during the night than during
the day, i.e at periods when Colomys is active, drifting animals occur frequently. These

drifting animals are assumed to be filtered from the flowing water with the help of the vibrissae. The peculiar structure at the base region of the vibrissae is presumed to allow the detection of very weak stimuli and it is postulated that drifting animals are perceived with the help of the vibrissae. Regarded from the front the distances between the vibrissae are approximately 0.5 mm, a "mesh size", which is frequently used by limnologists in drift studies. The fact that pupal exuviae and probably pharate imagines of Trichoptera were found in the natural diet, both very tpyical (surface-) drifts items, supports the idea that *Colomys* may be a passive filter feeder, at least a facultative one.

Passive filter feeders are common in running waters. However, they belong to the invertebrates. Of the vertebrates fishes are well known to feed on drift (e.g. BAILEY 1966; ELLIOTT 1973; METZ 1974), but to the best of our knowledge no mammal which feeds on the drift as a passive filter feeder in running waters has been reported up till now.

The observations in the laboratory show that *Colomys* is able to hunt its food actively. Of special interest is the fact that the prey organisms are detected in the water without *Colomys* being in direct contact with the prey. Again the peculiar vibrissae are regarded as the sense organ which enable this detection via water movements coming from the escaping prey. Even in the plastic basin this is a remarkable sensory performance, because, besides the water movements coming from the prey, there are a lot of other waves caused by the movement of *Colomys* itself, and the mouse must be able to "sort out" those from the prey organisms. In natural running waters the flow is always turbulent, even in shallow areas, and in this case such a sensory performance must be much more discriminative. Probably the problem of "sorting out" water movements coming from the prey is overcome by the special volume of the brain mentioned above. Further it may be possible that the sensory apparatus enable even the detection of the respiration currents made by gill or body movements of a lot of benthic invertebrates in running waters. Of all the benthic fauna known from the study area the respiration currents are expected to be strongest in case-bearing Trichoptera, which force the water out through the back opening of the case by means of undulatory movements of the abdomen. This may explain the heavy over-representation of case-bearing Trichoptera, which probably were picked up from the substratum (cf. below), in the natural diet of *Colomys*. The detection of such indistinct water movements are known from decapodes (TAUTZ and SANDEMAN 1980), which are able to perceive very low amplitudes of water particles.

Doubtless the underwater orientation of *Colomys* is well developed and prey can be detected without direct contact. These observations are in contrast to those of KINGDON (1974), who noticed that the sifting hands were used to search for the prey. These sifting movements were not observed in the *Colomys* kept in the laboratory. Nevertheless *Colomys* must be able to "work" under water, at least fixed pupae of Trichoptera are removed from the substratum, i.e. *Colomys* can collect the benthic fauna actively. The removal of fixed pupae of Trichoptera and of several benthic invertebrates, e.g. larvae of Psephenidae, Elmidae, or Heptageniidae, from e.g. stones needs some force. If the lotic component of the diet is not captured from the drift, *Colomys* must be able to do this work at fairly high current speeds.

At the present stage of knowledge it cannot definitely decided, whether *Colomys* is a passive filter feeder, an active hunter, or an active collector in its natural habitat – presumably it is able to feed in all the three ways. What can be definitely stated is that *Colomys goslingi* is a highly specialized predator in African running waters, which in any case exhibits remarkable sensory performances. This puts the species into an isolated position within the rodents, particularly if African ones are considered.