Ecology of African Small Mammals

Recent research and perspectives

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Introduction

In the early years of the century, most papers on African small mammals were descriptions of new species, and lists of the species at selected localities. Since then, new ideas and theories about ecology, and an increase in basic knowledge about African small mammals, have provided new ecological insights into how individuals, communities and species integrate with the environment. Such studies have been at local, regional and pan-African levels, and hence it is now possible to take a more holistic view of small mammals than was possible previously. Early studies on rodents were primarily on habitat preferences, demography, the use of tooth wear to indicate population structure, the influence of burning on populations, and reproduction (DELANY, 1972, 1986). These studies showed that, in many aspects of their life-histories, African rodents are capable of great flexibility and adaptability in relation to the short- and long-term changes in their environment. In contrast, the other "small mammals" – lagomorphs, bats, insectivores and elephant-shrews – have been studied to a much lesser extent. This paper surveys some of the most recent studies on small mammals and shows how these studies have provided African examples for some of the principal disciplines within ecology.

Order	Number of species	% of small mammals	% of total mammalian fauna of Africa *
Insectivora	173	22.2	16.2
Chiroptera	200	25.6	18.7
Rodentia	380	48.7	35.6
Lagomorpha	11	1.5	1.0
Macroscelidea	15	1.9	1.4
TOTAL	779	100.0	72.9

* = 1068

Table 1
The Numbers of Small Mammals in Africa
(Insectivora, Chiroptera, Rodentia, Lagomorpha, Macroscelidea).

How many species are there?

It comes as a surprise to many people that there are so many species of small mammals on the African continent (including the islands of the continental shelf). The five orders of small mammals comprise 73% of all mammals in Africa (Table 1; HAPPOLD, unpubl.). The most numerous are the rodents with 380 species, followed by the bats with 200 species. Such data does not tell anything about the numbers of each species, nor the geographical extent of each species; but it does serve to emphasise the huge species richness of the continent. The species richness of some orders of small mammals is far greater than for the larger better known species, for example the Artiodactyla (92 spp.), Carnivora (70 spp.) and Primates (99 spp.) (HAPPOLD, unpubl.). To place these numbers in context, the species richness in North America (from the far north to Panama, plus the Greater and Lesser Antilles) is (about) 54 species of Insectivora, 403 species of rodents, 192 species of bats and 25 species of Lagomorpha (calculated from data in HALL, 1981); thus Africa has about the same number of species of bats and rodents as North America, more Insectivora and fewer Lagomorpha.

Are African small mammals important?

The answer to this question obviously depends on your point of view. In terms of size, biomass, and the capacity to earn revenue for a country, they are not as important as the larger better known mammals. However, the sheer number of species, and the large population numbers of some of these species, deserve some measure of recognition. Small mammals are particularly important because of their multiple functional roles in the ecosystem. They occur in virtually all habitats, their feeding habits include grass-eaters, seed-eaters, carnivores, insectivores and fruit-eaters, their activities result in recycling of nutrients, they have many beneficial interactions with plants such as seed dispersal, seed germination and pollination of flowers, they modify local environments (« ecological engineering ») by their burrowing activities, and they provide food for many predators. Some species are reservoir hosts for micro-organisms which cause diseases in humans and domestic animals, and others are pests in agriculture and stored products. Bats are of value as predators of insects, and some species of rodents are utilised as food by humans. Thus small mammals have roles in most ecological systems and in all habitats, and many of their activities impinge on other animals, including humans (see HAPPOLD, 1995).

Recent studies on African small mammals

During the last decade or so, new biological techniques especially in relation to cladistics, cytogenetics and DNA analysis have resulted in many papers which investigate the genetical and evolutionary relationships within and between species and higher taxa. In order to get a rough idea of the main focus of research during the last five years (1994-1998 inclusive), the papers published in 10 journals were analysed in respect of taxonomic group(s) (orders, families) and subject.

Taxonomic categories	% of papers	Category as % of all small mammals
INSECTIVORA	7.5	22.2
Soricidae	4.8	
Chrysochloridae	2.7	
Erinaceidae	0	
CHIROPTERA	19.8	25.6
Megachiroptera	13.4	
Microchiroptera	6.4	
RODENTIA	59.8	48.7
Sciuridae	1.1	
Anomaluridae	1.1	
Muridae	39.0	
Bathyergidae	14.4	
Ctenodactylidae	0.5	
Hystricidae	2.7	
Thryonomidae	0.5	
Pedetidae	0.5	
LAGOMORPHA	1.1	1.5
MACROSCELIDEA	10.7	1.9
SEVERAL ORDERS*	1.6	1.6

* Papers where two or more of the above Orders are considered.

I Table 2
Publications on African Small Mammals – analysis of 187 papers published in ten Journals** (1994-1998) by taxonomic categories.

The journals selected were those which historically have published a wide range of papers on African small mammals. The largest number of papers considered the Rodentia (especially Muridae), followed by Chiroptera and Macroscelidea (Table 2). The number of papers for each taxon is not in proportion to the numbers of species in the taxa, e.g. the Rodentia is represented by more papers than justified by its numbers, and the Chiroptera and Insectivora by fewer papers.

Likewise, analysis by subject shows that ecological studies of various sorts comprise the majority of papers (Table 3). Field studies on single species and communities form the largest category (29%),

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** *Acta Theriologica, African Journal of Ecology, Biodiversity and Conservation, Journal of Mammalogy, Journal of Tropical Ecology, Journal of Zoology* (London), *Mammal Review, Mammalia, South African Journal of Zoology, Zeitschrift für Säugetierkunde.*

Subject	% of papers
Autecology	15
Community Ecology	14
Reproductive Ecology	17
Geographical ecology/surveys	8
Conservation Ecology	4
Behavioral Ecology	6
Taxonomy/systematics	6
Cytogenetics	10
Physiology	10
Morphology	10

Table 3
Publications on African Small Mammals – analysis of 187 papers published in ten Journals (see note of Table 2) (1994-1998) by subject. Papers on Feeding ecology are included in Autecology and Reproductive Ecology.

followed by reproduction (17%). Taxonomy and cytogenetics form 16%. Surveys and biogeographical studies appear to have declined in number in recent years, and there are few papers on conservation of small mammals.

Ecological studies

The remainder of this paper surveys some of the recent (and not so recent) ecological studies, and considers only some of the categories identified in the analysis given above. The ecological studies may be considered under six subdisciplines: autecology, community ecology, feeding ecology, reproductive ecology, geographical ecology and conservation ecology. The other categories in Table 3 are not considered in detail in this paper.

A word of caution is needed regarding the names of African small mammals. Ecological studies are often hampered by doubt as to the correct name, especially at the species level, of the animals under investigation. There are many examples of where a « single » species is now considered a complex of species (e.g. within the genera *Mastomys, Praomys* and *Hylomyscus*). The contrary situation also creates difficulties because what is actually a single species has been described, in the past, under a plethora of names, each one from a separate locality. A glance at the names of African mammals in WILSON and REEDER (1993) shows that synonymy is a very common occurrence. The ecologist, therefore, may have real difficulty in knowing the correct name(s) of the animals being studied. The problem may be overcome, to some extent, by placing specimens in a museum (so their identity can be re-assessed at a later date) and by pointing out the difficulties of nomenclature, if such exist, for the «species». Hopefully, these difficulties will be minimised in the future as a result of new methods of taxonomic analysis.

Autecology

Autecological studies are valuable in that they provide detailed information on a single species, perhaps in several parts of its range. The notable studies on selected bathyergids by JARVIS, BENNETT and their co-workers have provided detailed information on reproduction, colony structure and behaviour, and have shown how different members of this family vary in their characteristics according to sociality and location (e.g. BENNETT, 1994; BENNETT and JARVIS, 1995; BENNETT *et al.*, 1994; O'RIAIN and JARVIS, 1998). Likewise studies of *Praomys albipes* in Ethiopia (BEKELE, 1995; 1996), several species of *Gerbillus* (SHENBROT *et al.*, 1994, 1997), several species of elephant-shrews (KERLEY, 1995; LEIRS *et al.*, 1995; FITZGIBBON, 1997), *Beamys hindei* (FITZGIBBON *et al.*, 1995) *Saccostomus mearnsi* (KEESING, 1998a), *Mastomys natalensis* (LEIRS *et al.*, 1996, 1997), several species of gundis (GOUAT, 1985; GOUAT and GOUAT, 1987), and *Pipistrellus nanus* (HAPPOLD and HAPPOLD, 1996) – to name a few – have added to knowledge of these particular species. Most autecological studies have tended to be on species which are common and relatively easy to study. Lacking are studies of the less common and less widespread species about which we know practically nothing.

Community ecology

In recent years, studies on communities of animals living in one place have provided particularly valuable information on how different species have different habitat preferences, life-history strategies, demographic parameters, and reproductive strategies. These differ-

	Habitats				
	Grassland	Miombo	Mopane	Talus	Thicket
Number of species	8	8	4	4	2
Commonest species	*Mastomys natalensis*	*Tatera leucogaster*	*Aethomys chrysophilus*	*Aethomys namaquensis*	*Tatera leucogaster*
Species richness (hot wet – cool dry)	1.6 – 3.7	2.2 – 4.3	0.8 – 1.3	1.8 – 3.0	0.8 – 1.0
Species Diversity (hot wet – cool dry)	0.83 – 0.92	0.86 -1.39	1.25 - 0.54	0.56 – 0.86	0.65 – nd
Density (#/ha) (low- high)	0.2 – 36.7	2.1 – 10.0	1.6 – 33.0	8.2 – 32.1	0.8 – 4.1
Density ratio	1:183	1:5	1:20	1:4	1:5

Hot wet (Nov 1992-Apr 1993) — cool dry (May-Jul 1993) — nd : no data.

Table 4
Some characteristics of community structure of small mammals (data excludes *Paraxerus cepapi* which occured in all habitats except grassland) in Zimbabwe (data from LINZEY and KESNER 1997a, b).

ences are related to their different evolutionary histories and relationships, but show that there are many ways of survival under a particular set of environmental conditions, and that different localities may support quite different sets of species. Here, I will illustrate these ideas using some recent papers on rodents and on bats.

At the Sengwa Wildlife Research Area in Zimbabwe, there are five major plant habitats (Table 4). By studying the small mammals in each of these simultaneously, LINZEY and KESNER (1997a, b) were able to show that there were marked seasonal differences in the number of species, abundance and community structure in each of these habitats. Eleven species of rodents were recorded (excluding the sciurid *Paraxerus cepapi*), although there were only 2-8 species in each habitat. A single species occupied 1-4 habitats, although each species tended to prefer only one habitat. Comparison of habitats showed that each had a different species which was the most abundant species (except for miombo and thicket), different species richness and species diversity, and different densities. When population numbers increased (the timing of this varied slightly between species), maximum numbers for any particular species were attained in the habitat where it occurred when its numbers were low, i.e. as numbers increased a species did not invade a previously unoccupied habitat. Temporal variation (as measured by minimum and maximum numbers) was greatest in the riverine grasslands (as a result of the large numbers of *Mastomys natalensis*) and least in miombo, talus and thicket (where *M. natalensis* did not occur). The advantage of studying several habitats at the same time highlights the differences and variations between habitats and their mammalian faunas; what happens in one habitat is not necessarily (or usually) what happens in a neighbouring habitat. These findings are consistent with studies in other savanna habitats (HAPPOLD and HAPPOLD, 1990a, 1991) and illustrate a general pattern for small mammals in savannas.

Where the ranges of a number of species overlap, these species form a community. In theory, all species whose ranges overlap form a community; thus a millepede, a mouse, an antelope and an elephant form a community but since each of these species is so different to each other, most ecologists would regard this as stretching the meaning of "community" too far. However, a number of related species of rodents, or bats, or antelopes show a number of similarities due to their evolutionary relationships and each species may compete for resources with other species. So how do the species in a community fit together? Are there any rules which determine how many, and what sort of, species can co-exist? BROWN (1975) examined the communities of rodents in various deserts of SW America, and showed that in any one desert each species of rodent differed in weight (and many other characteristics); hence each species had slightly different requirements and abilities. Moreover, each of the communities showed the same pattern although the species involved were different.

An analysis of the 26 species of bats (HAPPOLD and HAPPOLD, unpubl.) living in Liwonde National Park in Malawi show a similar separation for within genus groups (Fig. 1) as did Brown's rodents. For example, there are five species of *Rhinolophus;* all vary in weight (by at least a factor of 1.2 as predicted by "Hutchinson's Rule"). The same is true for the other genera. Although some species have the same weights as other species, such similarity is only between species of different genera. Although weight is a very simple measure, different weights imply differences in size, wing area, wing loading, flight

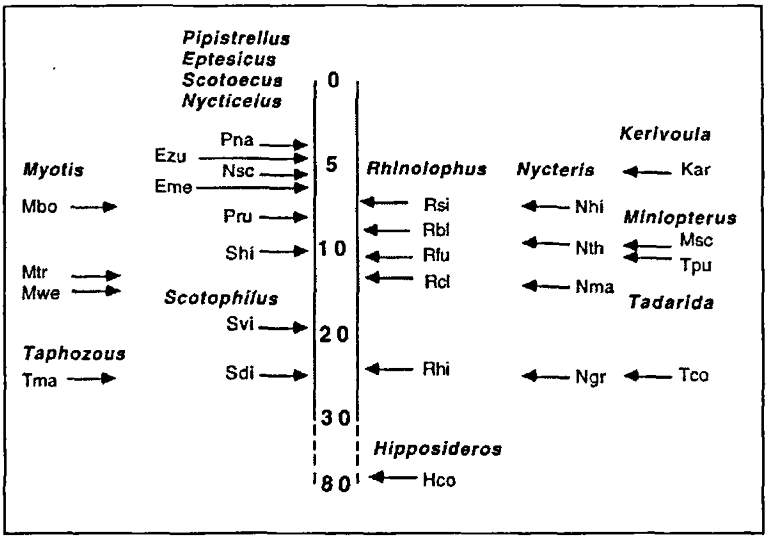

Figure 1
Community structure of insectivorous bats in Liwonde National Park, Malawi (as indicated by mean weight in grams) (M. and D. C. D. HAPPOLD, unpubl.).
Mbo = *Myotis bocagei*, Mtr = *M. tricolor*, Mwe = *M. welwitschii*,
Tma = *Taphozous mauritianus*, Pna = *Pipistrellus nanus*,
Pru = *P. rueppellii*, Ezu = *Eptesicus zuluensis*,
Eme = *E. melchorum*, Nsc = *Nycticeius schlieffenii*,
Shi = *Scotoecus hirundu*, Svi = *Scotophilus viridis*,
Sdi = *S. dinganii*, Rsi = *Rhinolophus simulator*, Rbl = *R. blasii*,
Rfu = *R. fumigatus*, Rcl = *R. clivosus*, Rhi = *R. hildebrandtii*,
Hco = *Hipposideros commersoni*, Nhi = *Nycteris hispida*,
Nth = *N. thebaica*, Nma = *N. macrotis*, Ngr = *N. grandis*,
Kar = *Kerivoula argentata*, Msc = *Miniopteris schreibersii*,
Tpu = *Tadarida pumila*, T. co = *T. condylura*.

characteristics, mouth size, and potential food. Thus the large number of species in this community can co-exist because of the many genera, and the differences between species within each genus and between genera. The bats of Kruger National Park (see ALDRIDGE and RAUTENBACH, 1987) are equally diverse, for the same reasons as given above. More information on other communities of bats in Africa, especially where there are many species, is required to confirm whether this is a general feature of African bats.

Genera [number of species]	Western Ghana [5]	Ghana [6]	Gambari Forest W. Nigeria [7]	M'passa Forest Gabon [8]	Irangi Kivu [9]	Mayanja Forest Uganda [13]
Praomys	***tullbergi***	***tullbergi***	***tullbergi***	*tullbergi*	***jacksoni***	*morio*
Malacomys	*edwardsi*	*edwardsi* *longipes*	*edwardsi*		*longipes*	*longipes*
Hybomys	*trivirgatus*	*trivirgatus*	*trivirgatus*	*trivirgatus*	*univittatus* *lunaris*	*univittatus*
Hylomyscus	*stella*	*stella*	*stella*	***stella*** *parvus*	*alleni*	*stella*
Lophuromys	*sikapusi*		*sikapusi*	*sikapusi*	*flavopunctatus*	*sikapusi* ***flavopunctatus***
Grammomys				*rutilans*		*dolichurus*
Stochomys		*defua*	*longicaudatus*			
Deomys				*ferrugineus*	*ferrugineus*	
Heimyscus				*fumosus*		
Aethomys						*kaiseri*
Lemniscomys					*striatus*	*striatus*
Mus						*triton* *minutoides*
Tatera						*valida*
Oenomys						*hypoxanthus*

Sources: Jeffrey 1977 (Ghana); Cole 1975 (Ghana); Happold 1977 (W. Nigeria); Duplantier 1989 (Gabon); Dieterlen 1985 (Kivu); Delany 1971 (Uganda).

I Table 5
Species of small rodents in selected rainforests to illustrate variation in species richness, species replacement and subsets.
The most abundant species in each rainforest is in **bold** print

Analyses of communities of rodents illustrate other aspects of how communities are structured. After surveying many communities of rodents (primarily in North America and Australia), Fox (Fox and Brown, 1993; Brown, 1995) suggested a series of « assembly rules » which were applicable to all communities. The three principal rules are: (a) different communities show character convergence (in contrast to "character displacement" within the community), (b) there is usually

Locality (number of species)	Abundance (%)				
	1st	2nd	3rd	4th	n
Gambari, Nigeria (7) [1]	75	10	3	2	482
Ghana (6) [2]	37	23	11	11	270
Ghana (5) [3]	57	20	14	5	194
Gabon (8) [4]	58	12	11	11	549
Ituri, Zaire (4) [5]	35	32	30	3	60
Kivu, Zaire (8) [6]	25	22	14	13	3541
Mayanja, Uganda (13) [7]	51	28	6	4	818
Mean values	48	21	13	7	

[1] HAPPOLD 1977; [2]; COLE 1975; [3] JEFFREY 1977; [4] DUPLANTIER 1989;
[5] GUBISTA 1999; [6] DIETERLEN 1985; [7] DELANY 1971.

Table 6
The four most abundant species of terrestrial rodents in primary rainforests expressed as the percentage of all individuals.

only one species per genus and a new genus is added to the community in preference to a second or third species within a genus, and (c) communities in different localities within region or biome consist of a series of nested subsets in which common abundant species are found in all communities and rare species occur only in certain communities where they are additional to the common species. Do these « assembly rules » apply to African rodents? Rainforests contain 5-13 species according to locality (Table 5); individuals of the single commonest species comprises about one half of the community and the two commonest species comprise about 70% of the community (Table 6). The remainder (i.e. 3 -11 spp.) comprise the remaining 30% and hence are uncommon or rare. Communities of small mammals within each of the forest « blocks » in rainforest zone of Africa (i.e. Western, West Central, East Central, South Central; see HAPPOLD, 1996) are unique in respect of their species composition (although there is greater similarity at the genus level), but nevertheless the functional characteristics of each community appear to be similar. Lists of species show that each genus is usually represented by only one species, and that certain genera and/or species are widespread

Locality (number of species)	Abundance (%)				
	1st	2nd	3rd	4th	n
Olokomeji, Nigeria (8) [1]	57	33	4	3	606
Igbo-Oro, Nigeria (6) [2]	62	10	10	8	48
Foro, Ivory Coast (10) [3]	47	24	10	10	3 900
Uganda (10) [4]	40	18	15	12	349
Kenya (9) [5]	77	7	7	3	1456
Liwonde, Malawi (7) [6]	47	19	18	8	106
Zimbabwe (11) [7]	35	31	14	5	313
Mean values	52	20	11	7	

[1] ANADU 1973; [2] HAPPOLD 1975; [3] GAUTUN 1975]; [4] CHEESEMAN 1975;
[5] KEESING 1998a; [6] HAPPOLD and HAPPOLD 1990a; [7] LINZEY and KESNER 1997a.

Table 7
The four most abundant species of terrestrial rodents in natural savanna expressed as the percentage of all individuals.

while others are very restricted (Table 5). For example, individuals of one species of the genus *Praomys* (*tullbergi, jacksoni* or *morio*) are always the most numerous or the second most numerous comprising 75-28% of all rodents, and individuals of the genus *Malacomys* (*longipes* or *edwardsi)* comprise 23-2.7% in the five forests where they occur. Some species (of the genera *Stochomys*, *Deomys*, *Oenomys*) are always rare if they occur at all. The abundance of *Lophuromys* (*sikapusi* or *flavopunctatus*) varies greatly according to the availability of damp grassy patches within the forest, in much the same way as the abundance of *Malacomys* depends on the availability of swampy areas. In savanna localities, there are 6-10 species and the most abundant species comprises 35-77% of individuals (Table 7). However, compared with the rainforest (Table 6), there are a greater number of species which may comprise the most numerous species; according to the locality, it may be *Lemniscomys* spp., *Myomys daltoni*, *Saccostomus* spp., *Acomys spinossisimus*, *Tatera leucogaster* or *Aethomys chrysophilus*.

	Makokou district Gabon (1)		Liwonde N. P. Malawi (2)		Kruger N.P. South Africa (3)	
	Genera	Species	Genera	Species	Genera	Species
Rodentia	22	31	11	11	19	20
Chiroptera	20	34	14	27	15	29

Sources: (1) HAPPOLD 1996 (based on Brosset 1966, 1969, 1988; DUBOST 1968, b; EMMONS *et al.* 1983). (2) ANSELL and DOWSETT 1988, HAPPOLD and HAPPOLD 1990b, D. C. D. & M. HAPPOLD unpubl. (3) PIENAAR *et al.* 1980.

Table 8
The numbers of genera and species of rodents and bats at three localities.

There are few localities where both rodents and bats together have been studied in detail. However where such data are available, such as at Makokou, Liwonde and Kruger (Table 8), bat communities have a greater species richness (and usually genus richness), and therefore greater complexity than do rodent communities. Rodents seem to conform more to the second of the assembly rules than do bats; the ratio of genus: species for rodents is 1:1 for Liwonde and Kruger and 1:1.4 for Makokou, but 1:1.7 and 1:1.9 for bats. Thus bat communities are able to accommodate more species per genus than rodents. The reasons for this are unclear although the larger pool of species and the three-dimensional environment of bats may be contributory reasons. The number of genera and species are a measure of the complexity of the habitat.

Thus, these « rules » are partially correct for African small mammals. Certainly there is character convergence at the genus and functional level for rainforest rodents and, likewise, for savanna rodents. Within the rodent communities of rainforest and savanna there is generally only one species for each genus, although in some situations there may be two species per genus, and the communities which contain only a small number of species are usually a subset (at the generic level) of communities with larger numbers of species. In contrast, the rodents of the northern (Sahara) and southern (Namib) desert and semidesert regions show a contrary community structure: each has its unique fauna, with no overlap in species composition although functionally they are similar. Within each fauna, there is character displacement; for example, the species of *Gerbillus* in the Sahara are the ecological equivalents of *Gerbillurus* in the Namib.

African bats, for the most part, do not conform to these « rules ». The limited evidence suggests that different communities exhibit character convergence, and in the larger communities there are many species per genus. Hence, each species shows strong character displacement. No conclusions can be made about nested subsets for bat communities; however, a study on bat communities in Tanzania (COCKLE *et al.*, 1998 – see later) suggest that they are not organised as subsets.

Feeding ecology

Analyses of stomach contents and faecal pellets has provided a lot of data on the diet of rodents. Many species of rodents have been shown to feed a wide variety of green vegetation and seeds, each being fairly specific in what it eats; others are omnivorous, some tend towards insectivory and carnivory. All tend to vary their diet on a seasonal basis in response to what is available. Regular sampling can provide a very detailed picture of the main constituents of the diet and the adaptability of a species. One example will suffice to illustrate a general trend in rodents. The Nile Rat *Arvicanthis niloticus* is a widespread species in moist savanna habitats. A study by RABIU and FISHER (1989) recognised four food categories – monocotyledons, dicotyledons, animal matter, and seeds (including grains); all four categories formed some part of the diet in most months, but the proportional contribution of each varied according to month and season (Fig. 2). During two dry seasons, monocotyledons and dicotyledons formed the main part of the diet (monocotyledons 51.7 and 38.9%, dicotyledons 32.5 and 41.2%). During the wet season, the proportion of monocotyledons and dicotyledons declined and the proportion of animal matter (27.7 and 31.7%) and seeds (15.7 and 39.9%) increased. This suggests that the rats show a preference for animal matter and seeds when available but eat a greater proportion of vegetation during the dry season when animal matter and seeds are less available. Although the pattern between the two successive years was similar, animal foods and seeds formed a smaller propor-

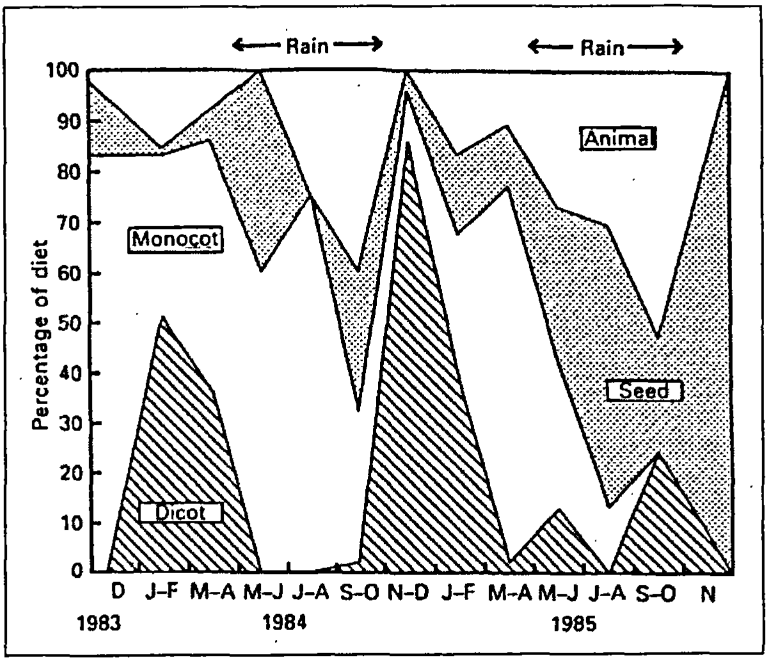

Figure 2
The diet of *Arvicanthis niloticus* in Kenya (RABIU and FISHER, 1989).

tion during the first year when rainfall was lower than during the second. The diet of Nile rats in Kenya (DELANY and MUNRO, 1986) showed a similar pattern in relation to wet and dry seasons, even though the length and timing of wet and dry seasons in Kenya are quite different to that in Nigeria. Flexibility of diet in relation to the timing and length of wet and dry seasons, and to variation between years, appears to be a general characteristic of small rodents. The Nile rat and other widespread species owe their success, in part, to their omnivorous and opportunistic feeding habits. In contrast, specialist feeders are less widespread and less successful.

Even within such broad categories as those given above, rodents need to be selective in order to maximise the amount of energy from their food. Because of their small size and relatively high metabolic rates, small rodents (and other small mammals) can not afford to spend time looking for and eating foods which provide only small amounts of energy. The Optimal Foraging Theory suggests that optimal diet maximises energy gain, and that mammals (small ones in particular) must select those foods, and parts of foods, that are high in energy. In addition, the energy (and time) spent in foraging and « handling » must be less than the energy gained from the food. Such ideas have rarely been tested on African small mammals. However, KERLEY and ERASMUS (1991) showed that *Gerbillus paeba*, *Mus minutoides* and *Mastomys natalensis* were selective when presented with 11 types of seeds. The rodents chose those seeds, or parts of seeds, which allowed the highest rate of energy intake and which required the least amount of « handling time ». For larger seeds, they ate only those parts of the seed which were high in energy. The smallest species, *Mus minutoides*, preferred seeds which could be eaten with the minimum of wastage, and avoided larger seeds which required long handling times.

The importance of food selection is provided by an experimental study on *Gerbillus henleyi* (mean wt 10g) and *Meriones crassus* (mean wt 73g) which live in the deserts of northern Africa (KHOKHLOVA *et al.*, 1997). Both species gained the majority of their energy intake from the millet seeds, but some energy (and water) was obtained from the saltbush (*Hammada salicornica*). However, gerbils ate only the young buds, located in the stem nodes, which are rich in energy; in contrast *Meriones* ate all parts of the plant including the fibrous stems. By careful selection of the buds, the gerbil maximises its energy and water intake from its plant food by selection of the most nutritious parts. These studies illustrate how experimental and laboratory studies are useful for understanding observations in the field.

Rodents show the same principles of food selection (although on a much smaller scale) as do the Artiodactyla (see JARMAN, 1974); large species (such as buffaloes and cane rats) can eat large amounts of food which may not necessarily be nutritious, but small species (such as duikers and small murids) must select only those parts of a plant, such as new shoots, fruits and seeds which are highly nutritious.

Shrews, elephant shrews and microbats are insectivorous, but there are few detailed studies on the precise nature of their diets. However, a study in the Namib desert showed that the diet of three species of shrews (*Crocidura fuscomurina*, *C. cyanea* and *C. hirta*) was primarily invertebrates (64.9 – 82.9% of the diet) but also included small lizards (DICKMAN, 1995). All three species were generalist insectivores, but each species selected a slightly different range of prey. *Crocidura fuscomurina* ate proportionally more Chilopoda, Araneidae, Coleoptera, Orthoptera and larvae, and fewer Collembola and Formicidae, than was expected from the frequency of these prey in the habitat; *C. cyanea* had a similar diet but with more Isoptera than expected and fewer Coleoptera, while *C. hirta* had a diet similar to *C. fuscomurina* but with fewer Orthoptera and more Isoptera. Thus each species had a diet composed of a different mixture of the available food items reflecting, in part, species-specific food selection and differences in the abundance of different food items in the habitats where each species foraged. Elephant shrews have traditionally been thought of as insectivores, although recent studies (KERLEY, 1995; SPINKS and PERRIN, 1995) show that many species are omnivores and include herbage in their diet. For example, *Elephantulus rufescens* has an almost entirely insectivorous diet (99% insects, 1% herbage), whereas herbage constitutes 18-49% of other species which have been investigated. The amount of herbage varies according to the time of year and the locality (KERLEY, 1995). Microbats, like shrews, are purely insectivorous although one species, *Nycteris grandis*, feeds also on small vertebrates (FENTON *et al.*, 1981). Each species of insectivorous bat shows careful food selection in respect of size and hardness of its insect prey, the location of the prey, and its flight characteristics. There are several classic papers on the diet of microbats which provide details on the diet of a number of species (e.g., FENTON *et al.*, 1977; VAUGHAN, 1977; ALDRIDGE and RAUTENBACH, 1987; FINDLEY, 1993). These examples of rodents, shrews, elephant shrews and bats indicate that small mammals select their food carefully and utilise many resources.

Reproductive ecology

Research on reproduction of African rodents had resulted in many papers; these have covered topics as varied as length of gestation, litter size, growth of young, variations in reproduction in relation to environment change, the relationship between reproduction and demography, and environmental stimuli for reproductive activity. Needless to say, the large species richness of rodents and the very

1.	All species have a species-specific well-defined period of reproduction, with a period of maximum reproductive activity. Period of reproduction may be short or long.
2.	Seasonal and yearly variations in rainfall and food at a single locality result in changes in the onset and termination of the reproductive period.
3.	Species with a large biogeographical range show flexibility in the timing and length of the reproductive period (from seasonal to aseasonal).
4.	Each species at a single locality has a different reproductive strategy, resulting in differing effects on the demography of the community.
5.	The reproductive period is mainly controlled by changes in climate (especially rainfall) and food availability and quality (especially proteins and oestrogenic compounds). Daylength and temperature are of lesser importance at lower latitudes than at higher latitudes.
6.	Females of most species are polytocous (2-10+ young/litter) and polyoestrous; have a post-partum oestrus, and a period of anoestrus.

I Table 9
Reproduction in African small rodents.

varied habitats and climates of Africa have resulted in a wealth of different methods of reproduction. However, the number of species for which there is detailed knowledge is limited; species which were well studied in recent years include *Mastomys natalensis* (DUPLANTIER *et al.*, 1996; FIRQUET *et al.*, 1996; LEIRS *et al.*, 1994), *Tatera leucogaster* (NEAL and ALIBHAI, 1991; NEAL, 1996), *Arvicanthis niloticus* (RABIU and FISHER, 1989), several species in the Sahel (SICARD and FUMINIER, 1996), and several species of bathyergids (e.g. BENNETT, 1994; BENNETT *et al.*, 1994). A few generalisation may be made from all this variety (Table 9).

Reproductive ecology in African rodents has been studied in two main ways: (a) field studies which record the times when adults are in reproductive condition and when young individuals enter a population, and (b) the effect of supplemental food on wild populations. There are many studies which have recorded the times of reproductive maturity and pregnancies for a range of species (see Table 2 in NEAL, 1991). All the features listed in Table 9 have a common goal: to maximise fecundity and to increase the chances of survival for the young. In rainforest, reproductive activity is strongly related to the seasonal pattern of rainfall which, by and large, is regular and predictable. For example, in Uganda and Zaire near the Equator where the wet season is extensive, reproduction may occur throughout the year (but with seasonal peaks of births) (e.g. DELANY, 1971; HAPPOLD, 1977). In West Africa, where the wet season is shorter, reproduction is mostly at the end of the wet season and the early part of the dry season (HAPPOLD, 1978, 1996). In savannas and semi-arid habitats where grasses and herbs are the principal foods, the months when conditions are good may be less predictable and rodents have to show more flexibility and opportunism. The period of reproduction may be limited to certain months when quality food and water are available (most species), but where food and water are not limited reproduction may be continuous (e.g. *Mastomys huberti* in flooded and riverine habitats (SICARD and FUMINIER, 1996)). In arid and semi-arid regions, reproduction is restricted to a few months (or weeks) when quality food and water are available, and temperatures are not too cold. There is considerable variation between different species at a single locality, and likewise species with a wide geographical range exhibit variations in their reproduction at different localities.

A particularly fruitful field of investigation has been the relationship between diet and reproduction. One of the best-studied genus in this respect is *Mastomys*. Various studies have shown that reproduction slows and stops during the dry season and that food *per se* does not necessarily initiate reproduction (Kenya: TAYLOR and GREEN (1976); Tanzania: LEIRS *et al.*, 1994; Senegal: HUBERT *et al.*, 1981). However, it seems very likely that new shoots from germinating seeds (as occurs at the beginning of the wet seasons) may be more important as a stimulant to reproduction than just the amount that is available (LEIRS *et al.*, 1994). Several studies on *Mastomys* (e.g. LEIRS *et al.*, 1994, MONADJEM and PERRIN, 1998; NEAL and ALIBHAI, 1991) have shown that supplemental food results in higher body weights. In southern Africa, supplemental food also resulted in higher densities of animals probably due to immigration and an increase in the number of males with scrotal testes, but did not stimulate reproductive activity in females (MONADJEM and PERRIN, 1998). As FIELD (1976) suggested long ago, quality is often more important than quantity. High quality food rich in protein and oestrogenic compounds is necessary for reproductive activity in both sexes, and does not usually become available until after the wet season begins. Hence it is not surprising that FIRQUET *et al.* (1996), LEIRS *et al.* (1994) and MONADJEM and PERRIN (1998) showed a correlation, for *Mastomys natalensis*, between reproductive activity and the rainfall one or two months previously. It is highly likely that such a correlation is a widespread occurrence and underlies the control of reproduction in many species; the variations on this basic theme are dependent on the amount and pattern of rainfall, absence of extreme heat or cold, and the time taken to produce quality food (whether germinating seeds, fruits or insects). Although photoperiod is considered an important environmental factor controlling reproduction in temperate environments, it is not considered of much importance in the tropics where annual differences in photoperiod are very slight. A full discussion on this topic may be found in DELANY (1986).

Development and growth of young rodents is also very varied. NEAL (1990) analysed the reproductive characteristics of many species of murid rodents, and showed that weight at birth (and many other reproductive characteristics) is strongly correlated with the adult body weight. The principal dichotomy in development and growth is between species which have precocial young and those which have altricial young. Precocial species (such as *Otomys* and *Acomys* spp.) have a longer gestation and fewer young in a litter, the young are heavier at birth and they have a slower postnatal growth rate than in altricial species. Most interestingly, altricial species living in arid and semi-arid regions (e.g. *Gerbillus* spp.), and arboreal folivores (e.g. *Thamnomys*) also have lower growth rates, perhaps due to an inadequate supply of high quality foods. Species within a subfamily often show similar characteristics; for example species of Dendromurinae and Gerbillinae tend to have shorter gestations and the young have lower birth weights than species in other subfamilies of equivalent weight. Studies such as this provide an interesting insight into how the various evolutionary lines of rodents have evolved. It would be interesting to look at other families of rodents in these respects, and to investigate the Lifetime Reproductive Success (LRS) of African rodents. Very little is known about longevity, fecundity, and survivorship of African small mammals and how LRS affects demography and abundance. One clue, as suggested by DUPLANTIER *et al.* (1996), is that species which are very fecund have the greater potential to expand their distribution compared with species with a lower fecundity; for example the higher fecundity of *Mastomys erythroleucus* in Senegal allows this species to spread more rapidly than *M. huberti* and *M. natalensis* which have lower fecundity.

Information on reproduction of bats is not as extensive as for rodents. Bats, like rodents, need to produce their young at a time which provides the best chance of survival for the young. An additional constraint is that female bats must remain aerodynamically efficient at all stages of pregnancy and while carrying new-born young. There is great diversity in the reproductive strategies: HAPPOLD and HAPPOLD (1990b) recognised 10 strategies based on the timing of parturition in relation to season, the presence or absence of reproductive synchrony, the number of pregnancies per year, and the presence or absence of post-partum oestrus. Several features of bat reproduction are worth mentioning:

(1) Most African microchiroptera have only one young/litter, and many have only one litter per year. Hence the annual productivity is low (contrary to most rodents). Whether this is compensated for by greater survival and greater longevity is uncertain.

(2) Usually, more than one strategy occurs within a geographical locality. In Malawi, for example, five strategies (Restricted Seasonal Monoestry, Extended Seasonal Monoestry, Seasonal Bimodal Polyoestry, Aseasonal Polyoestry, and Seasonal Multimodal Polyoestry) have been recorded in the 15 species for which there is adequate data.

(3) Some species of bats can change their chronology of reproduction by altering the interval between copulation and parturition; this may be achieved by sperm storage and delayed fertilisation (e.g. *Pipistrellus nanus* [BERNARD *et al.*, 1997]), delayed implantation (e.g. *Miniopterus schreibersi* [BERNARD *et al.*, 1996]), or retarded embryonic development (e.g. *Scotophilus borbonicus* [VAN DER MERVE *et al.*, 1988]).

(4) Most species in temperate regions and dry regions of Africa are monoestrous, although polyoestry is possible in those tropical regions where rain falls for most months of the year and insects are abundant for most of the year.

Geographical ecology

In contrast to many of the studies mentioned above which describe species or communities in a clearly defined locality, geographical ecology deals with the patterns and trends throughout the range of a species, a genus, a family or an order. It also seeks to understand how communities are structured, and how and why a taxon may change in abundance at different places within its range. BROWN (1995) has termed this subdiscipline « macroecology » implying that it is the large-scale patterns of distribution, rather than the fine detail, that enable a better understanding of the biogeography of animals.

There are many distribution maps for African mammals (Fig. 3); some record collecting and sighting localities (e.g. SETZER, 1956 for Sudan, HAPPOLD, 1987 for Nigeria) and others indicate presence/absence in quarter-degree squares (e.g. TAYLOR (1998) for Kwa-Zulu Natal, ANSELL and DOWSETT (1988) for Malawi, MONADJEM (1998) for Swaziland). A third method indicates the approximate range by shading or colour (e.g. SMITHERS (1983) for southern Africa, DORST and DANDELOT (1970) for Africa) but may include some areas where the species does not occur because the habitat is unsuitable. Whatever the range may be, it is a representation of various aspects of the ecology of the species and portrays an area where the vegetation, temperature, water availability and landscape ecology are within the tolerance of the species. Beyond this area, one or more « limiting factors » exceed the tolerance of the species preventing its permanent occupancy. Maps (on a fine and coarse scale) also indicate short-term historical and long-term evolutionary changes in distribution. The importance of good locality records (as provided by surveys and museum specimens) can not be over-emphasised. However, there are many species (and many countries) for which there are very little data. It may be too late to obtain reliable biogeographical data on some species because of the widespread destruction of many habitats in recent years.

When good data are available for many species in a region or a country, it is then possible to produce layer maps and identify « hotspots » of biological diversity. Good examples of this are recent studies in Namibia (Fig. 4; GRIFFIN, 1998) and in South Africa (GELDERBLOM *et al.*, 1995; GELDERBLOM and BRONNER, 1995; MUGO *et al.*, 1995) which clearly show that some areas contain greater species richness than others. Such hotspots are usually associated with high plant productivity and/or high plant diversity. Some ecologists have coined the terms « warmspots » and « coolspots » implying areas of lower biodiversity. Of course, areas of lower diversity (« coolspots ») may contain species and assemblages which do not occur in a hotspot, as

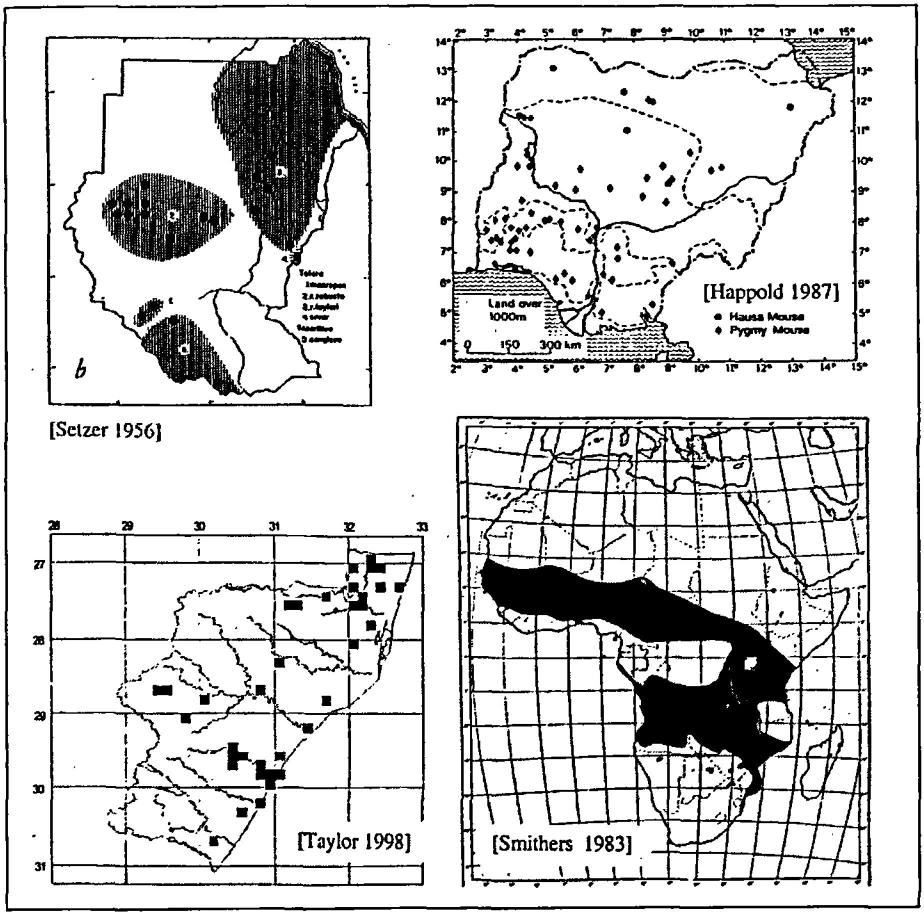

Figure 3
Examples of distribution maps for small mammals in Africa.
Top left: locality records and presumed distribution (SETZER, 1956);
top right: locality records only (HAPPOLD, 1987);
bottom left: presence in quarter degree squares (TAYLOR, 1998);
bottom right: general distribution without locality records (SMITHERS, 1983).

well as endemic species; such areas also require special conservation especially if they are not within a reserved area (GELDERBLOM and BRONNER, 1995). Thus knowledge of hotspots and of the distribution of species is necessary to identify localities of biological interest and conservation value.

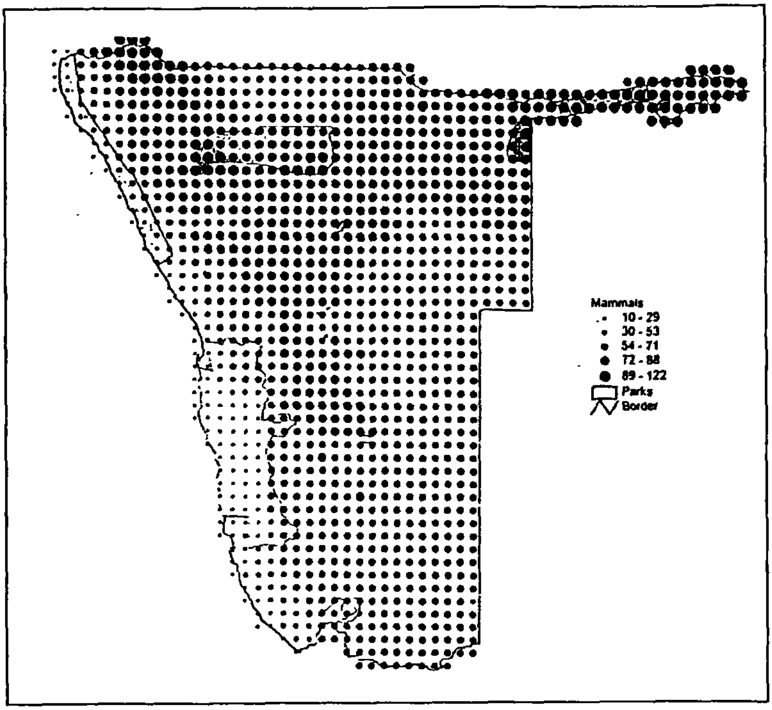

Figure 4
The number of species in quarter degree squares indicating variations in species richness – an example from Namibia (from GRIFFIN, 1998).

It is well known that different parts of the continent contain different assemblages of mammals. Travelling from east to west and north to south, from low altitudes to high altitudes, and from one vegetation type to another, there are slight (or major) discontinuities in the fauna. Species, genera and families decline in abundance, and other taxa take their place. Such changes can be analysed numerically (see e.g. HAPPOLD, 1987, and Fig. 5). For example, in Nigeria the number of species of rodents declines from south (rainforest zone) to north (Sahel savanna) whereas the Carnivora show the opposite trend, and the Artiodactyla have more species in the Guinea savanna than in the rainforest and Sahel savanna zones. Many situations in other parts of Africa could be analysed in a similar way. A different form of macrogeographical analysis is to look at the numbers of species of, for example, ungulates, carnivores, etc., in different regions of the conti-

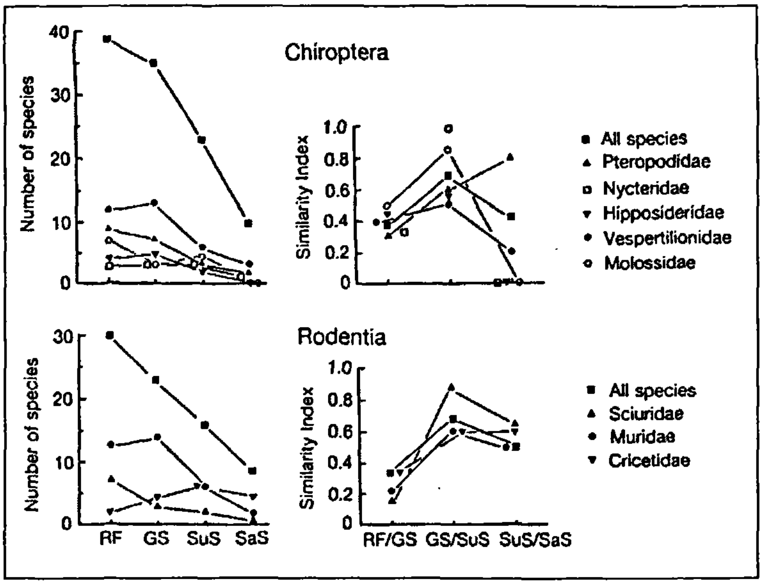

Figure 5
The number of species (left) and Similarity Index (right) of Chiroptera (top) and Rodentia (bottom) in Nigeria. Number of species: numerals indicate species numbers; RF = Rainforest, GS = Guinea savanna, SuS = Sudan savanna, SaS = Sahel savanna. Similarity Index: numerals indicate similarity between pairs of vegetation zones. 0 = no similarity, 1.0 = exact similarity. RF/GS = comparison between rainforest and Guinea savanna mammals, GS/SuS = comparison between Guinea savanna and Sudan savanna mammals, SuS/SaS = comparison between Sudan savanna and Sahel savanna mammals (from HAPPOLD, 1987).

nent (TURPIE and CROWE, 1994). Such analysis shows that the patterns of distribution correspond with the major vegetational biomes, and that the richness in each biome depends on the taxon. Different taxa attain their greatest species richness in different biomes: for Primates it is the central rainforests, for ungulates it is the east African savannas, and for carnivores it is the east and southern savannas. In general, richness is greatest close to the Equator, declining towards the higher latitudes. The complexity of distribution depends on the taxa; the ungulates have the greatest complexity (and hence the continent is divided into more regions each with its representative species) and the primates and carnivores have lesser complexities. The patterns for endemism do not necessarily follow the pattern for richness because endemism is a reflection of the past climates and vegetation (e.g. the Somali Arid Subregion has a high proportion of endemics in relation to its richness and area). There is great scope for similar studies on small mammals.

Another aspect of geographical ecology considers the distribution of communities, their likenesses and their differences. Bat communities tend to be more complex than rodent communities because of their greater species richness, and hence there is a greater degree of species packing (i.e. the niche for each species is narrower and more precise, and a greater number of species co-exist). An interesting example is provided by the bats living in the coastal forests of northern Tanzania (COCKLE *et al.*, 1998). Each of the 16 forests which were surveyed is fairly small (from a few tens of hectares to a few square kilometres); all are less than 600 m elevation, and the rainfall varies from under 1000 to about 2000 mm/year. A total of 46 species were recorded, but no more than 15 species were found in any one forest. For each of the eight forests which were surveyed in greatest detail, the number of species was 6-15, but why there were such differences is uncertain. Some forests tended to be dominated by rhinolophid bats, others by hipposiderid bats. The number of forests in which each species was recorded was also very varied: 20 species were caught in only one forest, 12 species were caught in two forests, and only two species were really widespread (*Hipposideros ruber* in 12 forests, and *Epomophorus wahlbergi* in 11 forests). The distribution of all 46 species is extremely patchy and does not seem to show any easily recognised pattern. Analysis of several other communities of African bats (HELLER and VOLLETH, 1995) showed that each varied in its species richness, and each had a mixture of morphological types (as indicated by aspect ratio and wingtip ratio). In some respects, the community structure was similar at each locality although there was great variation in the species composition. There are several important conclusions from these studies:

(1) Species richness and community structure of bats are extremely varied, and each species of bat may be associated with a different assemblage of bats at different localities.

(2) There are real and significant differences between neighbouring localities (clearly shown in the Tanzanian study) due to differences

in their ecology and/or evolutionary history. High species richness can occur at both a regional and a local level. Such richness at the local level has also been recorded in several other localities in Africa, such as in the Kruger National Park (PIENAAR *et al.*, 1980), at Masalani in Kenya (O'SHEA and VAUGHAN, 1980) and in Liwonde National Park in Malawi (Fig. 1) (see also HELLER and VOLLETH, 1995). High species richness and diversity may be the « normal » situation for bat communities in Africa.

(3) There is similarity in the community structure at different localities (despite differences in richness and composition) which suggests that the « rules » which govern bat communities are universal (perhaps with some exceptions?).

(4) The patterns of regional and local community structure has important implications for the conservation of bats.

Conservation ecology

In recent years, conservation of mammals in Africa has concentrated, correctly, on the larger species whose numbers have fallen rapidly and whose habitats are being destroyed and reduced in area. The decline in habitats and populations of many species is due, ultimately, to the increasing numbers of humans and the exploitation of the land for food production and resource exploitation (HAPPOLD, 1995). Conservation of small mammals is not usually considered as an important issue, in much the same way that conservation of large species was rarely considered in the first half of the 20th century. Nevertheless, there are many changes in land use which are equally adverse to small mammals as to large mammals (Table 10); many of these are interconnected. Any change in land use alters the desirability of the habitat for small mammals: most changes are deleterious (e.g. large scale agriculture and ranching, subsistence farming, removal of tree cover). Less well-known are the effects of plantations in former mixed woodlands and reforestation (where plantations replace grasslands – see ARMSTRONG and VANHENSBERGEN, 1996) because monocultures do not provide the variety of habitats and food which supported the original populations (HAPPOLD, 1987). Similarly, fragmentation of habitats from a large continuous areas to a series of isolated pockets reduces overall population numbers, isolates one population from

1	Increase in the numbers of humans and domestic animals.
2	Agricultural methods.
3	Timber extraction; reduction of forests.
4	Plantations of exotic trees.
5	Fragmentation of habitats.
6	Loss of specialised habitats.
7	Increased incidence of fires.

I Table 10
Ecological factors which have adverse effects
on small mammals in Africa.

another, and prevents movement of individuals between populations (see e.g. SAUNDERS *et al.*, 1987, USHER, 1987). A few species of small mammals have benefited from human activities however; for example *Mastomys natalensis* (which flourishes in agricultural fields and food stores), some species of *Tadarida* (which roost in human dwellings), and *Pipistrellus nanus* (which lives in furled banana leaves). It is wise to look ahead now and think about what measures may be taken to ensure adequate conservation of small mammals (Table 11).

Although African countries, in general, have a good record of established reserved areas (the average is about 7% [range 0 – 30%] of the landmass of each country), about 90% of the land is without any formal protection. WESTERN (1989) has pointed out that more attention must be given to conservation outside National Parks and Game Reserves, where in fact the majority of most populations of animals are living. Hence there needs to be better landscape management, i.e. promotion of vegetation along streams, reforestation with natural woodlands on slopes, protection of grasslands, and reduction of fragmentation by planting corridors to link fragments. The natural fauna (both mammals and other animals) will benefit by restoration of land to its former natural state by removal of exotic plants and animals, by elimination or reduction of humanized activities which gradually degrade the land, and by replanting with indigenous vegetation. Some of these initiatives are occurring in some African countries for more pragmatic reasons (such as improving water quality, preventing erosion and spread of weeds) than conserving small

1	More attention to be given to the 90% of land outside reserved areas.
2	Better landscape management.
3	Managed woodlands – natural and planted.
4	Restoration of habitats.
5	Exclosures.
6	Changes in burning policy.

Table 11
Initiatives for the conservation of small mammals in Africa.

mammals. Such initiatives should be applauded because, indirectly, they increase the biodiversity of the ecosystem and help to conserve small mammals. The suggestions made here must be co-ordinated within a total landscape policy which includes intensive agriculture, forestry, grazing lands and urban development.

Even in National Parks, simple procedures could enhance populations of small mammals. Most reserved areas were gazetted to protect the larger mammals, and anything else that lived or grew there was an added bonus. As far back as 1972, DELANY commented that populations of small mammals were lower in habitats which were overgrazed and overbrowsed by large mammals. Small mammals require a certain amount of cover, whether it be growing grass, presence of shrubs and thickets, leaf- and grass-litter, or fallen trees – and hence overgrazing and burning (NEAL, 1970; CHEESEMAN and DELANY, 1979) cause temporary reductions in populations. Protection of habitats by enclosures can form «mini-reserves» for smaller species; a good example of the effectiveness of enclosures is shown by KEESING (1998b) in Kenya who demonstrated that populations of *Saccostomus mearnsi* were twice as numerous inside enclosures, where there was no grazing pressure by wild ungulates and domestic cattle, than outside; other species showed similar trends but not so significantly. Protection within an enclosure also reduced episodic reductions of population numbers which were evident outside the enclosures. Reductions in the frequency of burning, to promote larger areas of unburnt grass and shrubs, will also encourage the increase in the numbers of small mammals.

Since each species responds differently to perturbations and protection, a mosaic of habitats with different levels of protection and management will promote the greatest diversity of small mammals both in reserved areas and in unprotected areas such as farmlands (HAPPOLD and HAPPOLD, 1997), forests (HALL, 1998) and ranches.

Future research

Although the last decade has produced many interesting ecological studies, research has been very uneven in respect of the species and countries. There are masses of studies on common and widespread species, and absolutely nothing on other species. Likewise, many studies originate in some countries, and very few in others. This discrepancy needs to be addressed, although it will be difficult because of the political instability, poor economy and lack of security in some countries. In many African countries, researchers have not been able to obtain modern equipment, or to have the chance to learn modern methodologies. One hopes that this will change in the near future. However, «simple» methods are still of great value, but they need better standardization so that studies at different localities (in the same and in different countries) are comparable. Ideally, research during the next decade should continue present initiatives and should focus on the following:

(1) Detailed surveys of communities with greater attention to structure, rather than just presence/absence. Such surveys may be at the local or regional level, and should be organised so that the results are comparative with other surveys.

(2) More information is required on the less common species and those with restricted biogeographical ranges. Likewise, collection of data and surveys of faunas should be encouraged in those countries which have not been extensively studied in the past. This will necessitate granting of funds and personnel by the richer well-endowed countries.

(3) There should be greater emphasis on experimental work to augment ecological studies, e.g. manipulation of habitats, addition of resources, and removal of species and individuals, followed by monitoring of

community composition, movements of individuals and other biological parameters. Such studies can determine the role of supposed « limiting factors » and provide evidence not obtainable by other means. Adequate replication is essential.

(4) Initiation of long-term studies which can follow complete cycles of demographic and ecological change. Some demographic cycles are short (e.g. rodents), but others are long (e.g. bats); such studies are essential for a proper understanding of the relationship between populations and their environments.

(5) Conservation-oriented research on rare and uncommon species, and on communities; identification of hotspots and habitats of special significance; the effects of habitat change on populations; formulation and implementation of methods to restore and increase the biogeographical ranges and populations numbers of species of small mammals.

(6) Analyses of pan-African or regional trends which help in an understanding of species and communities: their evolution, variations in biological characteristics in different environments, their current biogeographical ranges, and their interactions with other species.

Many of these suggestions for future research are not strictly ecological, but will involve physiologists, ethologists, taxonomists and geneticists. Such collaboration will enable a much more holistic view of the small mammals of Africa.

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