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Distribution patterns of terrestrial mammals in KwaZulu-Natal

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Distribution patterns, plotted by eighth-degree squares (7.5' × 7.5'), of the 162 mammal species recorded in the province of KwaZulu-Natal, South Africa were examined in relation to the combined factors of vegetation type, climate, and altitude (= bioregions); and in relation to protected areas within the nine bioregions. Highest species richness was recorded in the warmest most heterogeneous (vegetation) bioregions, and lowest in a cool montane region. Species richness was intermediate in relatively homogeneous, predominantly grassland bioregions. Mammalian biodiversity in KwaZulu-Natal is concentrated in the savanna regions in the north-east of the province, although further species-rich areas are found in the north-west and south-west for carnivores, and in the central region for many of the smaller mammals (Insectivora, Chiroptera, Rodentia). Analysis of taxonomic resemblances between bioregions distinguished taxonomically distinct 'savanna' and 'grassland' groups. Taxonomic resemblances between bioregions were generally lowest in bats (i.e. greatest bioregion specificity) and highest in carnivores (i.e. lowest specificity). In total, 92% of the mammal species occur in one or more protected areas. The percentages of species within protected areas in each of the bioregions are generally high (68–100%). In four of the bioregions the amount of land occupied by protected areas is adequate (6–96%) and protected areas are large, but in the other five bioregions the opposite holds (< 2% protected) and populations within them may not be viable.

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For the conservation of biodiversity, Stuart, Adams & Jenkins (1990) emphasised the importance of broad-based surveys as well as the assessment and recognition of key areas as steps towards understanding the inseparable aspects of genetic, species, and ecosystem diversity. The province of KwaZulu-Natal, by nature of its location between the warm Indian Ocean and the high Drakensberg range, contains a large variety of habitats and topographical differences. Conditions range between sub-tropical in the east and alpine in the west. In this report the distribution patterns of terrestrial, indigenous mammals are examined in relation to physiography, vegetation, and climate (= bioregions) in KwaZulu-Natal, as is the distribution of protected areas within the bioregions.

Most previous assessments of mammalian biodiversity in South Africa have relied on range maps from general texts, resulting in a map scale of one degree square or coarser (Rautenbach 1978; Siegfried & Brown 1992; Gelderblom 1993; Turpie & Crowe 1994). Gelderblom, Bronner, Lombard & Taylor (1995) analysed South African distribution patterns of species richness and endemism in three mammalian orders (Insectivora, Chiroptera and Carnivora) at a quarter-degree square (QDS: 15' × 15') map scale, based on some 12 500 museum specimen records, supplemented with literature records from regional texts. Mugo, Lombard, Bronner, Gelderblom & Benn (1995) used a similar approach to analyse the South African distributions of endemic or Red Data Book Rodentia, Lagomorpha and Macroscelidea. Freitag & Van Jaarsveld (1995) used both point data and range maps to assess mammalian biodiversity in the former Transvaal province. The present study considers all indigenous land-dwelling mammal species of KwaZulu-Natal at an eighth-degree square (EDS: 7.5' × 7.5') map scale, and is based on 7946 locality records comprising both museum specimens and sight records. Sight records obtained by Natal Parks Board staff members were used for the larger, more easily identifiable mammal species within orders such as Carnivora , Perissodactyla, Proboscidea, Pholidota, Tubulidentata and Artiodactyla. While Lombard (1995) argued for a national rather than a provincial approach to biodiversity assessment in South Africa, complete point data for all South African mammals are currently unavailable in digital form for the entire country; hence the present study is restricted to KwaZulu-Natal. Furthermore, the aim of the current study was to provide a rational basis for conserving mammalian diversity at a provincial scale in KwaZulu-Natal.

Study area

The province of KwaZulu-Natal, with an area of 91 800 km², lies between 26°45' and 31°10'S; 28°45' and 32°50'E (approximately 450 × 200 km). Altitude ranges from sea level in the east to over 3400 m on the Drakensberg in the west. Phillips (1973) recognised eleven groups of bioclimatic regions, based on physiography, vegetation, and climate. In this study seven of the original bioclimatic regions considered in relation to mammal distribution remain unchanged, namely: **Coast lowlands** (evergreen grassland, and tropical forest and thicket); **Coast hinterland** (grassland and semi-deciduous woody vegetation); **Mistbelt** of the midlands (grassveld and Afro-montane forest); **Moist upland** (tall grassveld and open savanna); **Drier upland** (tall grassveld and open savanna, but drier than the previous region); **Highland** (grassland with short, dense cover, and patches of Afro-montane forest); and

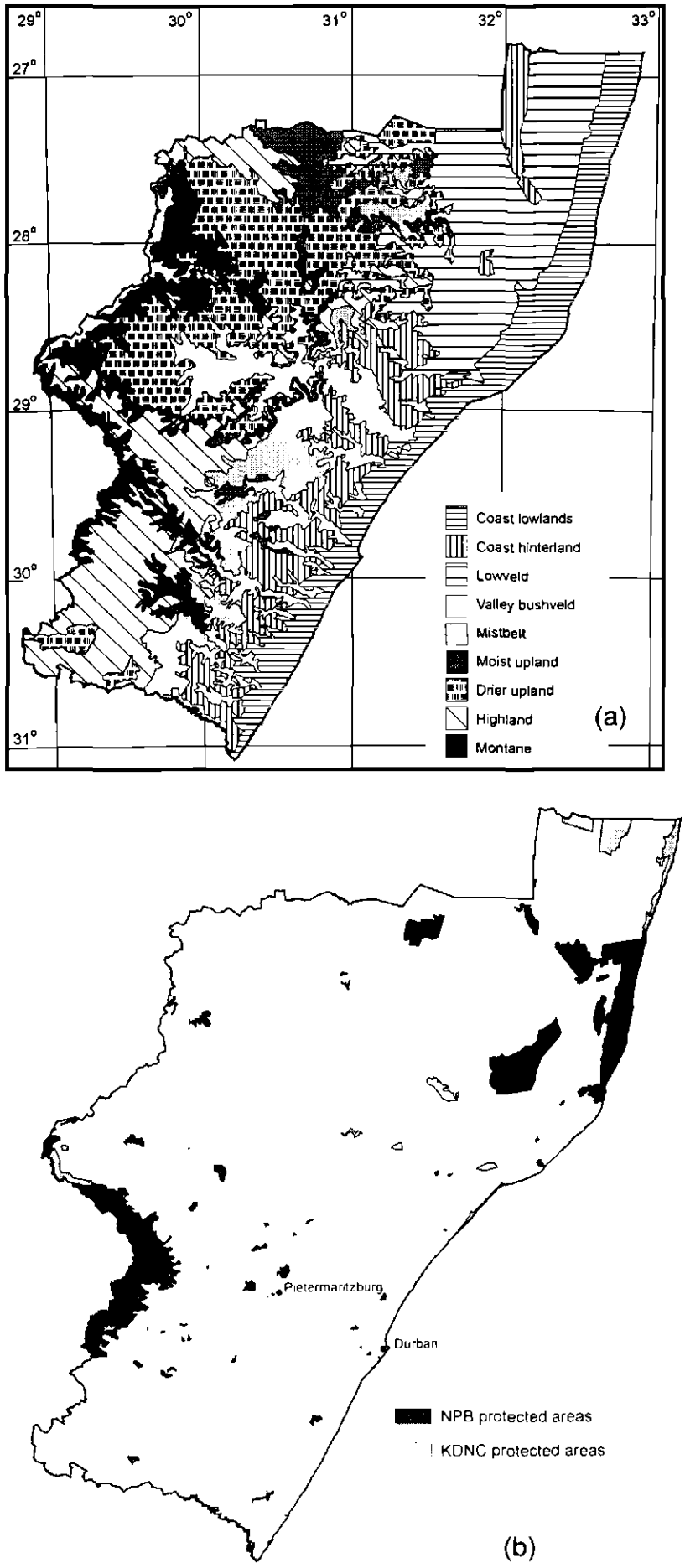

Figure 1 Distribution of bioregions (a) and formally protected areas (b) of KwaZulu-Natal. Bioregions based on bioclimatic regions (Phillips 1973) and bioresource units (Camp 1995).

Montane (temperate grassland and fynbos). The other four regions are grouped together as **Lowveld** (low-lying semi-deciduous and evergreen wooded areas of the north-east interior), and **Valley bushveld** (thicket and scrub, mainly *Acacia* spp., of the lower reaches of the major river valleys), based on veld types described by Acocks (1975) as well as a recently completed classification by Camp (1995). In this article the term 'bioregion' is used. Locations of the bioregions are indicated in Figure 1 and veld types are listed in Table 1a. We diverted from the original grouping by Phillips (1973) only by considering the low-lying wooded areas of the north-east separate from the wooded valleys south of about 28°30'S, as has been done by Camp (1995). Climatic characteristics of the different bioregions are given in Table 1b.

Formally protected areas in KwaZulu-Natal occupy 8.4% of the surface area: 6.7% under Natal Parks Board control and 1.7% administered by KwaZulu Department of Nature Conservation (Porter 1995). Protected areas are shown in Figure 1b.

Material and Methods

Detail on the distribution of indigenous terrestrial mammals in KwaZulu-Natal was obtained from Rowe-Rowe (1992 and 1994) for carnivores (museum specimen and sight records) and ungulates (mostly sight records), respectively; and from a data base maintained by PJT, containing museum records of mammals collected in the province. Distribution data for Rowe-Rowe (1992, 1994) were collected during the periods 1978–1991 and 1985–1993 respectively. By far the majority of museum specimens were collected between 1960 and 1995. In his distribution maps for the Insectivora, Chiroptera, Primates, Pholidota, Lagomorpha, Rodentia and Hyracoidea of KwaZulu-Natal (based mainly on museum records), Bourquin (1988) plotted pre-1968 records separately from post-1968 records. With the possible exception of one species of golden mole (see below under Results and Discussion), these maps showed no indication of errors owing to very old records from populations which may subsequently have become extinct.

Distribution data were obtained from the collections of the following museums: Durban Natural Science Museum, Kaffrarian Museum, Natal Museum, The Natural History Museum (London), South African Museum, Transvaal Museum. Records of small mammals (Insectivora, Chiroptera, Rodentia, Macroscelidea) were all based on museum specimens (apart from some 240 bats identified by C. Sapsford during a rabies scare in 1980 but not deposited in any museum); those of some larger mammals (Lagomorpha, Primates, Carnivorea, Hyracoidea) included both museum specimens and sight records; while virtually only sight records were used for Artiodactyla, Perissodactyla, Proboscidea, Tubulidentata and Pholidota. Lists of the protected areas from which each species had been recorded were obtained from a data base maintained by DTRR.

Taxonomy was based on Meester, Rautenbach, Dippenaar & Baker (1986), with slight modification: *Myosorex sclateri* was recognised as a full species distinct from *M. cafer* (Kearney 1993; Maddalena & Bronner 1992); *Amblysomus iris* was recognised as a subspecies of *A. hottentotus* (Bronner 1995); and *Amblysomus marleyi* was recognised as a full species (Bronner 1995).

A single data base including all 162 mammal species was compiled, listing distribution by eighth-degree squares, i.e. 7.5' × 7.5' or about 13 × 12 km. Point data, i.e. coordinates of

Table 1a Bioregions of KwaZulu-Natal, based on bioclimatic regions (Phillips 1973) and bioresource groups (Camp 1995), together with veld types (Acocks 1975) within each region

Bioregion	Phillips's numbers	Acocks's veld type No.	Name
Coast lowlands	1	1	Coast forest and thornveld
Coast hinterland	2	3	Pondoland coastal plateau
		5	Ngongoni veld
Lowveld	9, 10, 11	6	Zululand thornveld
		10	Lowveld
		11	Arid lowveld
Valley bushveld	7, 10	23	Valley bushveld
Mistbelt	3	8	North eastern mountain sourveld
		45	Natal mistbelt ngongoni veld
Moist upland	6	63	Piet Retief sourveld
		64	Northern tall grassveld
		65	Southern tall grassveld
		66	Natal sour sandveld
Drier upland	8	64	Northern tall grassveld
		65	Southern tall grassveld
		66	Natal sour sandveld
Highland	4	44	Highland sourveld
		54	*Themeda* veld to highland sourveld
		56	Highland sourveld transition
		57	North-eastern sandy highveld
Montane	5	58	*Themeda-Festuca* alpine veld

Table 1b Bioregions of KwaZulu-Natal and summary of their characteristics. Based on bioclimatic regions (Phillips 1973) and bioresource groups (Camp 1995)

Region	Altitude (m)	Annual rainfall (mm)	Temperatures °C* Winter Min	Winter Max	Summer Min	Summer Max
Coast lowlands	0–450	800–1200	10	24	21	32
Coast hinterland	450–900	750–1300	7	22	17	28
Lowveld	150–1000	550–900	12	24	22	32
Valley bushveld	0–900	620–720	4	17	22	30
Mistbelt	900–1400	750–1500	3	19	16	27
Moist upland	900–1400	700–1000	2	21	15	27
Drier upland	900–1000	720–760	3	24	15	31
Highland	1400–1800	700–1250	1	17	13	25
Montane	1800–3500	1200–1800	0	16	13	23[1]
			−7	10	6	18[2]

*Temperatures are mean daily minimum and mean daily maximum for the coldest month in winter and warmest month in summer.
[1] Measured at 1800 m.
[2] Measured at 3000 m.

latitude and longitude, were not used as they were not available for all species.

Distribution patterns and species richness were examined using MapInfo (Mapping Information Systems Corporation, USA). Distribution in relation to bioregions was determined by manually superimposing distribution maps of individual species on a map of the bioregions. In addition, computer analyses of distribution in relation to bioregions was performed using Lotus Approach (Lotus Development Corporation, USA).

Faunal affinities among bioregions were determined by UPGMA cluster analysis (Sneath & Sokal 1973) of Duellman's (1965) Faunal Resemblance Factor (FRF), calculated from the presence of species in bioregions determined by the manual overlay method. The manual overlay method was used as this was thought to be more meaningful than the computer method (see below under 'Distribution in relation to bioregions'). FRF was calculated manually for each pair of bioregions, as the number of shared species expressed as a proportion of the mean of number of species present in the two bioregions being compared. Cluster analyses were performed separately for all mammals, and for the five largest orders: Artiodactyla (29 species), Carnivora (32 species), Insectivora (18 species), Chiroptera (36 species) and Rodentia (30 species). For the purpose of the above analyses (but not for analyses of species richness), occurrences owing to introductions of species to areas outside of their former range were omitted. The above approach does not take into account species densities in different bioregions. To accommodate density, species occurrences expressed as percentages of the total number of squares occupied by each bioregion could be analysed using UPGMA analysis of coefficients of association, such as the Bray-Curtis and Euclidean distance (see Gelderblom *et al.* 1995). However, as discussed below, quantitative density data determined from computer analysis in the present study overestimated the distribution of taxa within each bioregion owing to the coarseness of the map scale relative to the detailed boundaries of bioregions. For these reasons UPGMA was based only on binary data in this study.

Data on areas occupied by veld types and the sizes of protected areas were obtained from Porter (1995).

Results and Discussion

Species richness

Species richness within KwaZulu-Natal is indicated for all mammals combined, and for the five largest orders, in Figure 2. The remaining eight orders which contain between one and four species are dealt with at the end of this section. A complete list of species, together with the bioregions in which each was recorded, is provided in Appendix 1.

The overall distribution pattern for all mammals (Figure 2a) indicates a generally higher species richness in the north-east of the province, where 36 of the 54 hotspots (darkest-shaded squares indicating 31–64 species) are located. In both the north-east and the southern portions of the province, centres of highest species richness coincide with protected areas in which surveys have been done, with two exceptions; in the vicinities of the major urban centres of Pietermaritzburg and Durban. We believe that the higher species richness in the north-east is not solely an artefact of the presence of protected areas, but is related also to their location in the richer Lowveld bioregion and the northern Coast lowlands (Table 2). Extensive mammal surveys have been conducted in the large Natal Drakensberg Park (Montane and Highland biore-

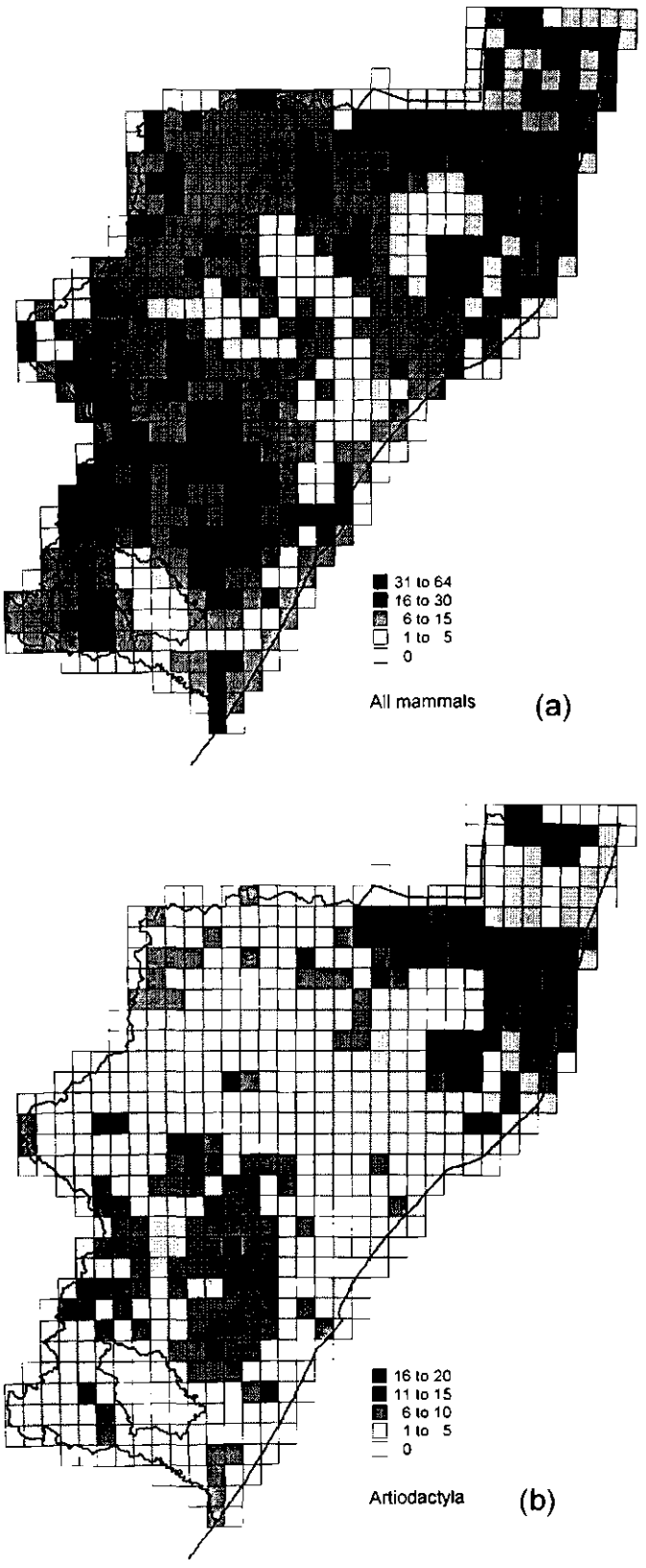

Figure 2 Patterns of species richness of all mammals (a); Artiodactyla (b).

gions) along the western border of KwaZulu-Natal, where 59 species have been recorded. However, in the three large protected areas of the north-east (Greater St Lucia Wetland Park, Hluhluwe-Umfolozi Park, Itala Game Reserve), the numbers of mammal species recorded are higher, respectively 97, 82 and 80.

A similar pattern to that reflected for all mammals is evident among Artiodactyla (Figure 2b). The single high-density square in southern KwaZulu-Natal includes a private nature reserve where additional artiodactyls have been introduced.

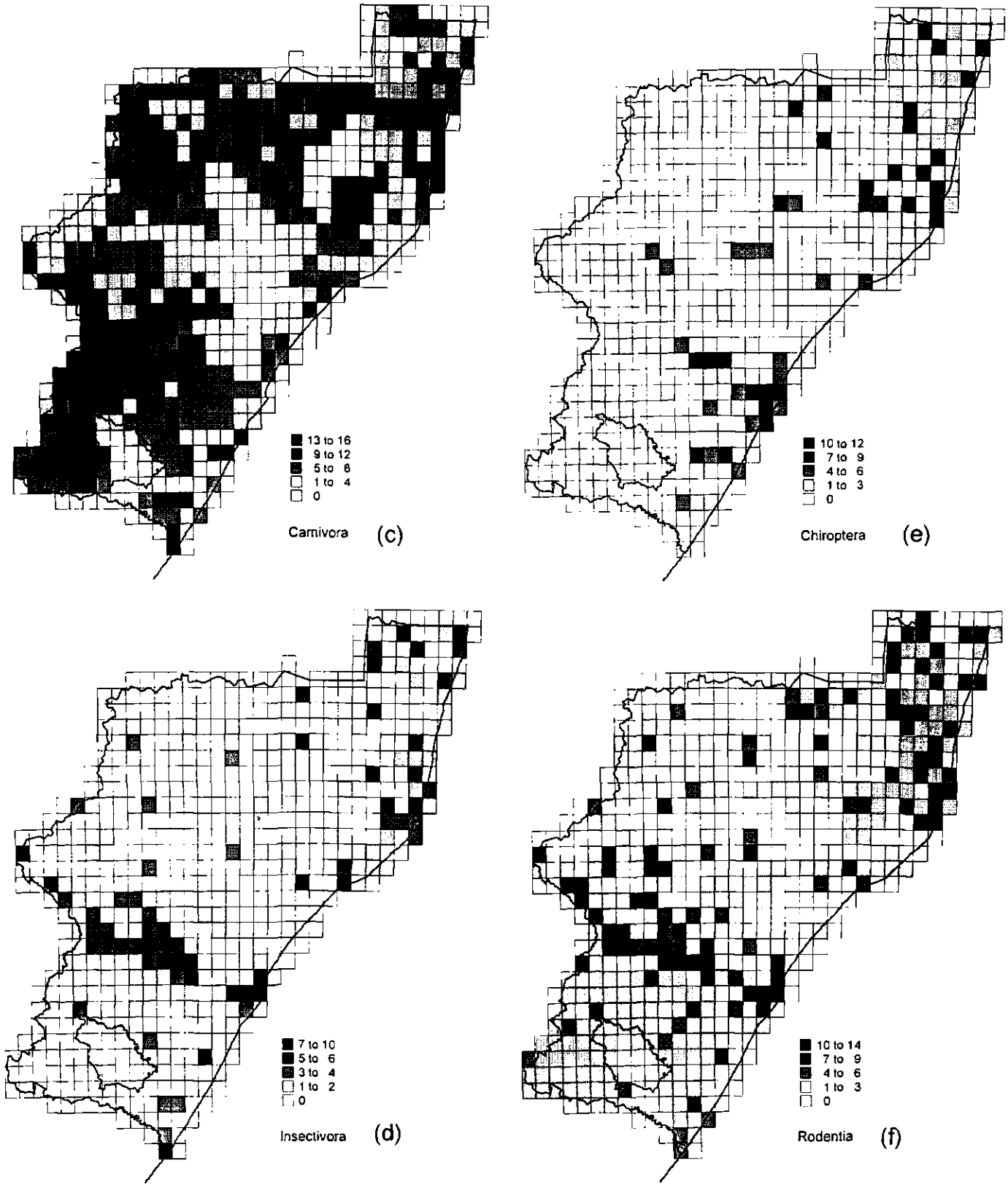

Figure 2 (Continued). Patterns of species richness: Carnivora (c); Insectivora (d); Chiroptera (e); and Rodentia (f) in KwaZulu-Natal. The keys indicate the number of species per EDS. The highest category indicates the hotspots.

Table 2 Numbers of species of mammals, by taxonomic orders, recorded by manual overlay in the bioregions of KwaZulu-Natal. CL = Coast lowlands; CH = Coast hinterland; LV = Lowveld; VB = Valley bushveld; MB = Mistbelt; MU = Moist upland; DU = Drier upland; HL = Highland; MT = Montane

Order (*n* species)	CL	CH	LV	VB	MB	MU	DU	HL	MT
Artiodactyla (29)	18	12	22	20	9	12	21	11	9
Carnivora (32)	21	14	22	18	12	16	20	18	14
Chiroptera (36)	23	21	28	16	9	6	9	4	2
Hyracoidea (2)	2	1	1	1	2	1	1	1	1
Insectivora (18)	14	13	14	7	11	5	5	10	3
Lagomorpha (3)	2	2	2	2	2	3	3	3	2
Macroscelidea (2)	1	0	1	1	0	0	1	0	0
Perissodactyla (3)	2	2	3	3	1	1	2	1	0
Pholidota (1)	1	0	1	0	0	0	0	0	0
Primates (4)	4	1	4	4	3	1	2	1	1
Proboscidea (1)	1	0	1	0	0	0	0	0	0
Rodentia (30)	26	17	24	19	13	15	17	19	14
Tubulidentata (1)	1	1	1	1	1	1	1	1	0
Total (162)	116	84	124	92	63	61	82	70	46

The pattern of increased species richness in the north-east would be even more obvious if it were not for many introductions of artiodactyls (i.e. species which did not formerly occur) to other parts of the province; particularly to the north-west and south of the province (Rowe-Rowe 1994), where the number of native species is much lower than that in the north-east, but where between 6 and 10 species have been widely introduced and become established (Appendix 1).

The Carnivora (Figure 2c) show two centres of high species richness: the north-east and the south-west. A third centre, with slightly lower species richness occurs in the north-west. Rowe-Rowe (1992) found that 11 carnivore species were confined mainly to the north-east and coast, nine were exclusive to the south-west, seven were confined mainly to the north-west (Drier upland bioregion), and five were widespread. These centres of species richness which are reflected in the present study were not evident in the QDS scale analysis of South African carnivore distributions (Gelderblom *et al.* 1995), owing to the use of the coarser resolution used by these authors.

Distributions of the smaller mammals (Insectivora, Chiroptera, Rodentia) (Figure 2d–f) are based on museum specimens and are therefore more likely to suffer from biases in collecting intensity than are the distributions of larger mammals based on sight records. Relatively few specimens were collected prior to the 1960s, reducing the possibility of data distortions owing to very old specimens from local populations which may have subsequently become extinct as a result of changing land-use practices. One possible exception may be the rough-haired golden mole, *Chrysospalax villosus*, of which 19 out of 23 known museum records date from between the 1900s and mid-1950s. Judging from the scarcity of modern records (and the widespread occurrence of this species from a number of archaeological sites throughout KwaZulu-Natal from 10000 to < 1000 years BP: Avery 1991), the range of this species in KwaZulu-Natal has contracted considerably during both pre-historical and historical times.

Species richness maps for all three of the above orders show centres of high species richness in the central region of KwaZulu-Natal, largely associated with the metropolitan centres of Durban and Pietermaritzburg. To some degree this reflects greater sampling intensity owing to the location of mammal collections at the Durban Natural Science Museum and (until recently) the Natal Museum in Pietermaritzburg, as well as active Zoology or Biology departments at the University of Natal's Durban and Pietermaritzburg campuses. Species richness is further enhanced by the benefit some species gain from man-made habitats such as houses (e.g. certain roof-dwelling bat species including *Scotophilus dingani*, *Tadarida* spp. and *Otomops martiensseni*) and suburban gardens and parks (e.g. *Crocidura flavescens*, *Suncus* spp., *Epomophorus wahlbergi*, *Mastomys natalensis*, *Mus minutoides*, and *Graphiurus murinus*).

The occurrence of a north-east centre of species richness in Chiroptera and Rodentia, cannot be explained by the level of sampling, and reflects the relatively high number of species found in the savanna habitats of the Lowveld and northern Coast lowlands bioregions (Table 2). Gelderblom *et al.* (1995) found species richness in Chiroptera to be highest in savanna habitats in the north-east of South Africa, including the Kruger National Park and smaller centres in KwaZulu-Natal, Gauteng, and Eastern Cape. This richness results from the presence of tropical species which intrude only marginally into the northern and eastern regions of South Africa, including the Lowveld, northern Coast lowlands and Valley bushveld bioregions of KwaZulu-Natal. In KwaZulu-Natal many tropical species reach their southern distributional limits in the north-east savanna regions of Maputaland (e.g. the bats *Tadarida ansorgei* and *Cloeotis percivali*, and the golden

mole *Calcochloris obtusirostris*) and Zululand (e.g. the four-toed elephant shrew *Petrodromus tetradactylus*, the bats *Nycteris hispida* and *Chalinolobus variegatus*, the red squirrel *Paraxerus palliatus* and the red duiker *Cephalophus natalensis*). A number of bat species (e.g. *Rhinolophus simulator, Hipposideros caffer, Miniopterus fraterculus*) extend their ranges southwards by exploiting Valley bushveld habitats associated with the major east-flowing rivers such as the Mgeni, Tugela and Mfolozi.

Apart from the central KwaZulu-Natal centre of insectivore species richness, species-rich squares seem to be scattered (largely owing to poor collecting) mostly in the Coast lowlands and Coast hinterland in the moister, eastern parts of the province. There is no north-east centre of richness, as was found in other small mammals (bats and rodents).

In the Insectivora, Gelderblom *et al.* (1995) found that South African centres of species richness occurred in the more mesic north-eastern areas in Northern Province, KwaZulu-Natal, and Eastern Cape, often coinciding with mountainous or forested areas receiving high precipitation. They postulated that finer scale analyses would reveal the importance of forest habitats for insectivore diversity. The availability of such habitats in the midlands region of KwaZulu-Natal (e.g. forested areas within the Karkloof Mountain Range) suggests that factors over and above sampling intensity may explain high insectivore (and other small mammal) species richness in this region (Figure 2d). Another factor could be the narrowness of the coastal plain in the central region, giving rise to rapid changes in altitude, climate and vegetation over relatively small geographical distances, accounting for increased habitat (and consequently faunal) heterogeneity. Indeed, a number of bioregions (Coast hinterland, Moist upland, Mistbelt, Valley bushveld and Highland) are closely juxtaposed and interdigitated in this region (Figure 1a).

Distribution patterns of species in the remaining eight orders are as follows: Proboscidea are confined to portion of the Lowveld and northern Coast lowlands bioregions where elephants have always occurred (Tembe Elephant Reserve), or where they have been reintroduced. The three perissodactyls are also concentrated in the north-east: all of those south of the Lowveld and northern Coast lowlands having been introduced to localities outside of their former range (Rowe-Rowe 1994; Appendix 1). The four primate species occur at highest richness in the north-east and around the forests in the south, but are generally absent from most of the Drier upland bioregion. Of the two Hyracoidea, *Procavia capensis* is widespread in suitable habitat mainly at midland and highland elevations, whereas *Dendrohyrax arboreus* is confined to certain forests in Mistbelt and southern Coast lowlands. The single member of the Tubulidentata, *Orycteropus afer*, is widespread (Appendix 1), whereas the only species of Pholidota, *Manis temminckii*, is very rare and confined to northern Coast lowlands and Lowveld. No overlap occurs between the two Macroscelidea: *Elephantulus myurus* is confined mainly to rocky habitats in Drier upland while *Petrodromus tetradactylus* occurs in dune forests of northern Coast lowlands and northern Lowveld (Appendix 1). Of the three Lagomorpha, two (*Lepus saxatilis* and *Pronolagus rupestris*) are relatively widely distributed throughout the province (although the latter is more restricted in its requirement for rocky habitats) while *P. crassicaudatus* has a scattered and localised distribution.

An area of low species richness for all of the orders is evident in the lower and middle reaches of the Tugela River valley, most obvious in Carnivora (Figure 2c). It is in this portion of the province that dense, rural human settlement has taken place and virtually no mammal collecting has been done. More detailed sampling may reveal the presence of more species.

Distribution in relation to bioregions

The numbers of species recorded in each of the bioregions (determined by manual overlay method) are summarised by orders in Table 2.

The data obtained from both computer analysis (not shown) and manual overlays (visual assessments) indicated that overall species richness by bioregion was highest in Lowveld, followed by Coast lowlands, and lowest in Montane. The rank order of the other bioregions differed, however, as did the number of species in each, being markedly higher in the results of the computer analysis.

Percentage differences in number of species between computer-generated data and those from visual assessments were lowest in Lowveld and Coast lowlands (7% and 9% greater in computer-generated assessments), the bioregions which are most compact in shape. In the other bioregions that are interdigitated or fragmented, or both (Figure 1a), differences ranged between 26% and 102% more species in computer-generated data. A count of the number of bioregions falling within each square revealed that in only 104 (16%) was only one bioregion present. In 474 of the squares (73%) either two or three bioregions were present. A single distribution record by eighth-degree square would, in the computer analysis, likely be accredited to two or more bioregions. In the visual assessment examinations, however, personal judgement was used. For example: if an eighth-degree square distribution record overlapped portions of three bioregions, one of which was bushveld and the other two were grassland, but it was known that the species involved occurs only in bushveld, it was not accredited to the other two bioregions.

Our opinion is that in this study species richnesses based on computer analysis are exaggerated, while those determined by visual assessments and personal knowledge (Table 2) are closer to reality, with perhaps slight under-representation. Accurate results would have been achieved with the computer analyses if all distribution records in the data base had been entered by geographic co-ordinates and analyses done on point data.

Species richness determined by visual assessment conforms to the expected in relation to habitat heterogeneity (Pianka 1966; Simpson 1966; Dueser & Brown 1980). Highest species richness was recorded in the most heterogeneous bioregion (Lowveld), followed by the Coast lowlands then Valley bushveld. The more homogeneous, predominantly grassland bioregions of Coast hinterland, Mistbelt, Moist upland, Drier upland, and Highland have similar species richnesses; while richness in the high-altitude, markedly cooler (equates to higher latitudes) Montane bioregion is lowest. The

general pattern is that species richness decreases in the province both from north to south and from east to west.

Greater numbers of mammals were recorded from the northern portion of Coast lowlands (roughly north of 28°30') than from the southern portion. Possible reasons may be that the northern section has suffered less from both loss and alteration of habitats than has the south; a number of species reach their southernmost limit of distribution in the north, adding to the species richness; and more land lies within protected areas than is the case in the south. It has also been hypothesised that the width of the coastal plain plays a role: as the width of the plain diminishes so too does its carrying capacity for both number of individuals as well as number of species (Stuckenberg 1969). However, as discussed above under 'Species richness', this may not apply to small mammals, where habitat heterogeneiety resulting from the compression of different bioregions into a narrower zone may enhance species richness.

Faunal affinities of bioregions

Matrices of Faunal Resemblance Factors (FRF) (Table 3) and phenograms based on these coefficients (Figure 3) indicate faunal resemblance of bioregions for all mammals, as well as for the five largest orders.

Gelderblom *et al.* (1995), analysing distribution by QDS, demonstrated marked differences in South African biome (Rutherford & Westfall 1986) specificity between orders, with Insectivora showing the greatest biome specificity (lowest values for taxonomic resemblances; mean FRF = 0.441) and Carnivora being the most generalised (highest values for taxonomic resemblances; mean FRF = 0.816). In the present study, bats (Chiroptera) showed the highest specificity to bioregions (lower resemblances; mean FRF = 0.352; Table 3e), probably because of the steep decline in species richness from warmer low-lying 'savanna' habitats (Lowveld, Coast lowlands and Valley bushveld) to colder, higher altitude grassland habitats (Montane, Highland, Moist upland), as shown in Table 2. Insectivore bioregion faunas were much more closely related (mean FRF = 0.621; Table 3d) than in the study by Gelderblom *et al.* (1995), probably because of the higher number of South African endemic Insectivora compared to KwaZulu-Natal which has only two endemic insectivore species (*Myosorex sclateri* and *Amblysomus marleyi*). On the other hand, Carnivoran species showed higher bioregion specificity in KwaZulu-Natal (mean FRF = 0.700; Table 3c) than was the case for South African biomes (mean FRF = 0.816). This can be explained by the fact that, while many Carnivoran species have large pan-African distributions (Turpie & Crowe 1994), a number of species reach their distributional limits in KwaZulu-Natal owing to the convergence of temperate (drier and moister grassland habitats) and tropical (savanna habitats) faunas in the province, giving rise to three centres of richness (north-east, north-west and south-west), as discussed above.

The Lowveld bioregion is taxonomically close (FRF > 0.717) to Coast lowlands in all mammal groups (Figure 3 a–f). Valley bushveld is fairly closely related (FRF > 0.600) to this group (Lowveld and Coast lowlands) in Artiodactyla (Figure 3b), Chiroptera (Figure 3e) and Rodentia (Figure 3f), while Coast hinterland is related to this group in the Insectivora (Figure 3d) and Rodentia (Figure 3f). The taxonomic association observed between 'savanna' bioregions such as Lowveld, the northern Coast lowlands and Valley bushveld, is due to the marginal intrusion into north-east KwaZulu-Natal of tropical mammal species, as discussed above under 'Species richness'. On the other hand the Montane bioregion appears to resemble taxonomically (FRF > 0.700) the Moist upland (all mammals, Artiodactyla, Carnivora, Insectivora) or Highland (Rodentia) bioregions. However, in bats the Montane bioregion is unrelated to any other bioregions (mean FRF = 0.157), and contains only two species (Table 2, Figure 3e). The Montane, Highland and Moist upland bioregions together comprise a 'moist pure grassland' association which tends to cluster separately from the 'savanna' association comprising Coast lowlands, Valley bushveld and Lowveld (Figure 3). The Coast hinterland and Mistbelt bioregions are taxonomically closely related (FRF > 0.800) to one another in all cases except for Insectivora (Figure 3d) and Chiroptera (Figure 3e), but they cluster within both 'grassland' (all mammals, Artiodactyla, Carnivora, Rodentia) and 'savanna' (Insectivora, Chiroptera) groups.

There are at least 35 species which are typical of the savanna association: too many to list here, but see Appendix 1. Of these, some are very rare, reaching their southernmost limit of distribution in north-eastern KwaZulu-Natal, e.g. the carnivores *Civetticus civetta*, *Helogale parvula*, and *Paracynictis selousi*; the mole *Calcochloris obtusirostris*; and at least four bats *Cleotis percivali, Chalinolobus variegatus, Nycticeius schlieffenii*, and *Tadarida ansorgei*. In the pure moist grassland association there are only five typical species: *Connochaetes gnou, Damaliscus dorcas, Pelea capreolus, Chlorotalpa sclateri*, and *Otomys sloggetti*. There are some others which occur predominently in pure moist grassland, e.g. *Aonyx capensis, Lutra maculicollis, Ourebia ourebi*, and *Poecilogale albinucha* (Rowe-Rowe 1992; 1994). The drier grassland association is characterised by species typical of more arid regions, reaching their easternmost limit of distribution in KwaZulu-Natal, e.g. *Galerella pulverulenta, Genetta genetta, Pedetes capensis*, and very rarely *Felis nigripes* and *Otocyon megalotis*. Other species typical of more arid regions, that occur predominently in drier grassland are *Elephantulus myurus, Cynictis penicillata, Vulpes chama*, and *Raphicerus campestris*.

The bioregions of Coast hinterland and Mistbelt contain a number of species which occur also in either savanna associations or grassland associations, e.g. *Cercopithecus mitis, Dendrohyrax arboreus, Ourebia ourebi, Philantomba monticola, Taphozous mauritianus*, and *Suncus lixus* (see also Appendix 1). The bat *Myotis welwitschii* is the only species recorded solely from Coast hinterland (Taylor 1991).

Distribution in relation to protected areas

Of the 162 mammal species recorded in KwaZulu-Natal, 149 have been found to occur in at least one of the province's protected areas. In Table 4 species recorded within protected areas in each of the bioregions are expressed as percentages of the total number of species recorded within each particular bioregion.

The Montane bioregion enjoys most protection, with almost the entire region and possibly 100% of the known

Table 3 Taxonomic resemblances (FRF) of the mammalian faunas of nine bioregions in KwaZulu-Natal. CL = Coast lowlands; CH = Coast hinterland; LV = Lowveld; VB = Valley bushveld; MB = Mistbelt; MU = Moist upland; DU = Drier upland; HL = Highland; MT = Montane

	CL	CH	LV	VB	MB	MU	DU	HL	MT
(a) All species									
CL	–								
CH	0.741	–							
LV	0.826	0.646	–						
VB	0.701	0.688	0.700	–					
MB	0.632	0.791	0.533	0.619	–				
MU	0.539	0.662	0.489	0.637	0.696	–			
DU	0.533	0.615	0.540	0.716	0.560	0.645	–		
HL	0.541	0.597	0.495	0.617	0.667	0.698	0.681	–	
MT	0.415	0.688	0.405	0.567	0.577	0.740	0.602	0.737	–
(b) Artiodactyla									
CL	–								
CH	0.636	–							
LV	0.743	0.444	–						
VB	0.592	0.526	0.688	–					
MB	0.545	0.857	0.444	0.526	–				
MU	0.381	0.615	0.385	0.556	0.769	–			
DU	0.462	0.556	0.516	0.609	0.556	0.706	–		
HL	0.308	0.444	0.387	0.522	0.556	0.706	0.727	–	
MT	0.333	0.500	0.483	0.667	0.625	0.800	0.800	0.800	–
(c) Carnivora									
CL	–								
CH	0.788	–							
LV	0.829	0.667	–						
VB	0.703	0.750	0.650	–					
MB	0.710	0.846	0.529	0.625	–				
MU	0.686	0.733	0.526	0.765	0.786	–			
DU	0.579	0.667	0.536	0.811	0.512	0.686	–		
HL	0.703	0.750	0.550	0.833	0.733	0.824	0.811	–	
MT	0.667	0.714	0.500	0.625	0.769	0.867	0.667	0.812	–
(d) Insectivora									
CL	–								
CH	0.889	–							
LV	0.857	0.815	–						
VB	0.667	0.700	0.667	–					
MB	0.750	0.783	0.667	0.588	–				
MU	0.526	0.556	0.421	0.667	0.667	–			
DU	0.526	0.556	0.526	0.833	0.667	0.600	–		
HL	0.667	0.609	0.583	0.706	0.900	0.667	0.667	–	
MT	0.235	0.375	0.235	0.600	0.462	0.750	0.500	0.462	–
(e) Chiroptera									
CL	–								
CH	0.711	–							
LV	0.717	0.625	–						
VB	0.634	0.611	0.636	–					
MB	0.412	0.621	0.378	0.240	–				
MU	0.312	0.444	0.343	0.348	0.250	–			
DU	0.303	0.500	0.389	0.417	0.118	0.400	–		
HL	0.207	0.333	0.250	0.200	0.308	0.364	0.333	–	
MT	0.074	0.091	0.133	0.222	0.000	0.200	0.200	0.333	–
(f) Rodentia									
CL	–								
CH	0.791	–							
LV	0.960	0.732	–						
VB	0.844	0.889	0.837	–					
MB	0.684	0.896	0.611	0.774	–				
MU	0.683	0.750	0.667	0.706	0.815	–			
DU	0.714	0.667	0.700	0.800	0.571	0.581	–		
HL	0.711	0.667	0.651	0.632	0.759	0.765	0.571	–	
MT	0.550	0.645	0.526	0.606	0.692	0.759	0.533	0.788	–

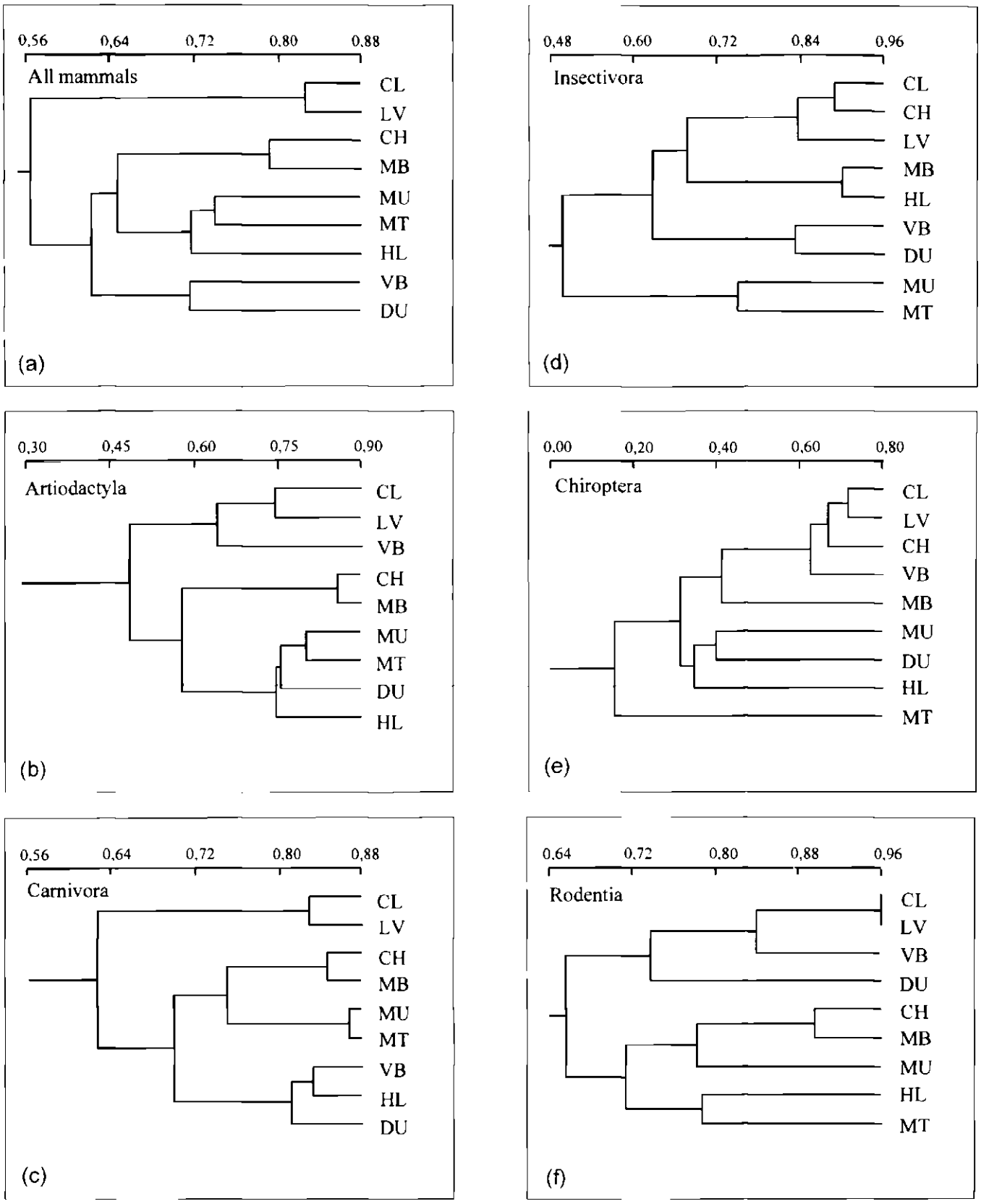

Figure 3 Faunal affinities of bioregions in KwaZulu-Natal as indicated by UPGMA cluster analysis of Duellman's (1965) Faunal Resemblance Factors (FRF) for all mammals (a); Artiodactyla (b); Carnivora (c); Insectivora (d); Chiroptera (e) and Rodentia (f). Cophenetic correlation coefficients were 0.697 (a), 0.803 (b), 0.704 (c), 0.778 (d), 0.868 (e) and 0.722 (f).

mammal species being within formally protected areas. Furthermore, the contiguous protected areas of the Natal Drakensberg Park form a single protected unit of Montane bioregion in excess of 1 000 km^2.

The proportions of Coast lowlands, Lowveld, and Highland in protected areas, as well as the percentages of each

Table 4 Areas of the bioregions of KwaZulu–Natal, expressed as percentages of the area of the province; percentages of each region within Natal Parks Board and KwaZulu Department of Nature Conservation formally protected areas; the numbers of mammal species recorded in protected areas as percentages of the total number of species recorded from each bioregion; and the numbers of small (< 10 km²), medium (10–100 km²), and large (> 100 km²) protected areas or portions of protected areas in each bioregion

Bioregion	% of province	% bioregion protected	% species protected	Protected areas (*n*) S	M	L
Coast lowlands	16	10.9	86	11	7	1
Coast hinterland	9	1.4	68	4	6	0
Lowveld	17	11.0	94	0	1	5
Valley bushveld	9	0.8	90	5	1	0
Mistbelt	5	1.0	79	3	3	0
Moist upland	8	0.8	80	1	2	0
Drier upland	17	1.5	91	2	2	1
Highland	17	6.0	89	14	4	1
Montane	2	95.6	100	0	0	1

bioregion's species recorded within the protected areas, appear to be adequate (Table 4), particularly as the sizes of single areas under protection are large: 700–2600 km². In Coast hinterland, Valley bushveld, Mistbelt, Moist upland, and Drier upland the proportions of land within protected areas are low. With the exception of Coast hinterland, however, the percentages of species within protected areas appear to be high. On the negative side, protected areas in the last-mentioned five bioregions are small: Coast hinterland 1–32 km²; Valley bushveld 5–41 km²; Mistbelt 1–12 km²; Moist upland 3–40 km²; and Drier upland 5–158 km². Populations of some mammals in these small areas may not be viable.

What is not known are the proportions of the bioregions outside of protected areas that are pristine or near-pristine. This is an aspect which is currently receiving attention. In a province such as KwaZulu-Natal in which there are only a few large protected areas and many small reserves (Figure 1), habitat conservation outside of protected areas is particularly important to reduce the effects of fragmentation, and to allow for movement in the event of global climate (and possible subsequent vegetation) change. In the five bioregions in which the proportions occupied by protected areas are low, greatest loss or modification of natural habitat appears to have taken place in Coast hinterland, Mistbelt, and Moist upland. In Drier upland and Valley bushveld there appears to have been less disturbance.

Priority taxa and areas of regional conservation importance

Based on the present spatial analysis of distributions, species of particular regional (and national) conservation importance are those which are either endemic to (90% or more of their range within) KwaZulu-Natal or are, within South Africa, found exclusively or mostly within KwaZulu-Natal, as well as species which occupy habitats which are either restricted in distribution, unprotected and/or are threatened by negative human or other impacts. The present study has indicated that mammalian species are reasonably well protected in KwaZulu-Natal (Table 4: 68–100% of the mammalian fauna of different bioregions occur in protected areas). However, individual species which are exceptions to this rule require further consideration.

Two species of mammals are endemic to KwaZulu-Natal: Marley's golden mole *Amblysomus marleyi* has been recorded only from the Ubombo District in the Lowveld bioregion and Sclater's forest shrew *Myosorex sclateri* occurs throughout Zululand. While *Myosorex sclateri* occurs in at least five protected areas, *Amblysomus marleyi* does not occur in any reserves, and its habitat is subject to degradation owing to overgrazing and increasing human populations. This species requires special conservation action by regional nature conservation agencies.

A further six species are, within South Africa, found exclusively in KwaZulu-Natal: the large-eared free-tailed bat *Otomops martiensseni* is restricted to the greater Durban region (Richardson & Taylor 1995), Ansorge's free-tailed bat *Tadarida ansorgei* is recorded only from Mkuzi Game Reserve, the hairy slit-faced bat *Nycteris hispida* is known from isolated records in northern Zululand, the Damara woolly bat *Kerivoula argentata* is known from isolated records in Maputaland and Zululand, Rendall's serotine bat *Eptesicus rendalli* has been recorded only from Bonamanzi Private Nature Reserve (Mondi Forests) in Zululand and the red squirrel *Paraxerus palliatus* occurs along the coast from the Mozambique border as far south as Lake St Lucia, with an isolated population in the Ngoye Forest. Of the above species, *Otomops martiensseni* is perhaps most in need of immediate conservation action, owing to the vulnerable nature of its habitat (roofs of old Durban houses which are frequently subject to fumigations for wood borer) and the fact that it does not occur in any protected areas.

Four additional species are, within South Africa, found predominantly in KwaZulu-Natal, with isolated populations occurring within the former Transvaal province: the yellow golden mole *Calcochloris obtusirostris*, Anchieta's pipistrelle *Pipistrellus anchietae*, the four-toed elephant shrew *Petrodromus tetradactylus* and the red duiker *Cephalopus natalenis*.

Species which have restricted distributions in KwaZulu-Natal, or are known to be rare in the province, but which occur fairly widely elsewhere in South Africa, include the rough-haired golden mole *Chrysospalax villosus*, the bats *Epomophorus crypturus, Eidolon helvum, Myotis welwitschii, Nycticeius schlieffenii, Rhinolophus swinnyi*, and *Cloeotis percivali*, the Cape molerat *Georychus capensis*, the pangolin *Manis temmincki*, the side-striped jackal *Canis adustus* and the dwarf mongoose *Helogale parvula*. As discussed above, *Chrysospalax villosus* may be declining in abundance, and as such this Vulnerable species (Smithers 1986) merits further research and conservation action at both provincial and national level. Apart from KwaZulu-Natal, this species is known only from restricted areas of the Eastern Cape, Mpumalanga and Gauteng. Many of the larger carnivores and ungulates are restricted to protected areas in KwaZulu-Natal, are intensively managed, and have distributions which have been altered owing to translocations as discussed above.

These species are not discussed further here (see Rowe-Rowe 1992, 1994).

Further information on the above aspects, as well as information relating to the South African Red Data Book status (Smithers 1986) and the extent of occurrence of KwaZulu-Natal's mammal species outside KwaZulu-Natal and South Africa, can be found in Bourquin (1988) and Rowe-Rowe (1992, 1994). Ultimately, species conservation plans should be based not only on spatial information but on demographic and population viability studies. Nevertheless, spatial studies assist by alerting conservationists to potential conservation problems and prioritising taxa for more detailed biological analysis.

The best conserved habitats in KwaZulu-Natal are montane grasslands (Montane bioregion) and 'savanna' (e.g. Lowveld and Coast lowlands; Table 4). The latter region corresponds to an important hotspot of mammalian biodiversity in the province. In this regard, the recent proclamation of the Greater St Lucia Wetland Park is of obvious importance to the conservation of biodiversity. The drier grasslands of western KwaZulu-Natal (Drier upland bioregion) are very poorly protected (1.5% of the province; Table 4) and yet are important for conserving the more arid elements of the province's mammalian fauna, particularly a local Carnivoran hotspot (Figure 3c). The Drier upland bioregion should therefore merit high priority in the placement of future protected areas in the province. In spite of obvious biases in collecting effort, the Durban and Pietermaritzburg metropolitan centres appear to be hotspots for Rodentia, Insectivora and Chiroptera (i.e. small mammals), underlining the importance of maintaining existing urban networks of natural areas such as the Durban Metropolitan Open Space System (DMOSS).

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Appendix 1 Bioregions in which each species was recorded. CL = Coast lowlands; CH = Coast hinterland; LV = Lowveld; VB = Valley bushveld; MB = Mistbelt; MU = Moist upland; DU = Drier upland; HL = Highland; MT = Montane. Open circles = introduced species

Order and species	CL	CH	LV	VB	MB	MU	DU	HL	MT
Artiodactyla									
Aepyceros melampus	○	○	●	○			○		
Alcelaphus buselaphus			●	●	●	●	●	●	●
Antidorcas marsupialis						○	●	●	
Cephalophus natalensis	●		●						
Connochaetes gnou					○	○	○	●	
Connochaetes taurinus	○	○	●	○		○	○		
Damaliscus dorcas		○	○		○	○	○	●	
Damaliscus lunatus							○		
Giraffa camelopardalis	○		○	○			○		
Hippopotamus amphibius	●		●						
Hippotragus equinus					○		○		
Hippotragus niger				○		○			
Kobus ellipsiprymnus	●		●	○			○		
Neotragus moschatus	●		●						
Oreotragus oreotragus			●	●			●		●
Ourebia ourebi	●	●			●	●	●	●	●
Pelea capreolus								●	●
Phacochoerus aethiopicus	●	○	●	○			○		
Philantomba monticola	●	●	●	●	●				
Potamochoerus porcus	●	●	●	●	●				
Raphicerus campestris	●		●	●			●		
Redunca arundinum	●	●	●	●	●	●	●	●	●
Redunca fulvorufula			●	●		●	●	●	●
Sylvicapra grimmia	●	●	●	●	●	●	●	●	●
Syncerus caffer	●		●	●			○		
Taurotragus oryx			●	●			●	●	●
Tragelaphus angasii	●	○	●	○			○		
Tragelaphus scriptus	●	●	●	●	●	●	●	●	●
Tragelaphus strepsiceros	●	●	●	●			●		

Appendix 1 Bioregions in which each species was recorded. CL = Coast lowlands; CH = Coast hinterland; LV = Lowveld; VB = Valley bushveld; MB = Mistbelt; MU = Moist upland; DU = Drier upland; HL = Highland; MT = Montane. Open circles = introduced species (Continued)

Carnivora									
Acinonyx jubatus	○		●				○		
Aonyx capensis	●	●	●	●	●	●	●	●	●
Atilax paludinosus	●	●	●	●	●	●	●	●	●
Canis adustus	●		●						
Canis mesomelas	●	●	●	●	●	●	●	●	●
Civettictis civetta	●		●						
Crocuta crocuta		●	●	●			●		
Cynictis penicillata				●		●	●	●	
Felis caracal	●	●		●	●	●	●	●	●
Felis lybica	●		●	●		●	●	●	●
Felis nigripes							●		
Felis serval	●	●	●	●	●	●	●	●	●
Galerella pulverulenta							●	●	●
Galerella sanguinea	●	●	●	●	●	●			
Genetta genetta						●	●		●
Genetta tigrina	●	●	●	●	●	●	●	●	●
Helogale parvula			●						
Herpestes ichneumon	●	●	●		●	●		●	●
Hyaena brunnea	○			●			●	●	
Ichneumia albicauda	●	●	●	●	●	●	●	●	●
Ictonyx striatus	●	●	●	●		●	●	●	●
Lutra maculicollis				●	●	●		●	●
Lycaon pictus			●						
Mellivora capensis	●		●	●					
Mungos mungo	●		●						
Otocyon megalotis							●		
Panthera leo			●						
Panthera pardus	●	●	●	●			●	●	
Paracynictis selousi	●		●						
Poecilogale albinucha	●	●			●	●		●	●
Proteles cristatus	●	●	●	●	●		●	●	
Vulpes chama				●		●	●	●	
Chiroptera									
Chalinolobus variegatus	●		●						
Cloeotis percivali			●						
Epomophorus crypturus		●			●				
Epomophorus wahlbergi	●	●	●	●		●			
Eptesicus capensis	●	●	●	●			●	●	
Eptesicus hottentotus			●	●					
Epetisicus rendalli	●		●						
Eptesicus somalicus			●						
Hipposideros caffer	●		●	●					
Kerivoula argentata	●		●						
Kerivoula lanosa			●						
Miniopterus fraterculus	●	●	●	●	●	●	●		
Miniopterus schreibersii	●	●	●	●			●		

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	CL	CH	LV	VB	MB	MU	DU	HL	MT
Myotis tricolor	●	●		●			●		
Myotis welwitschii		●							
Nycteris hispida	●								
Nycteris thebaica	●	●	●			●	●		
Nycticeius schlieffenii	●		●	●					
Otomops martiensseni	●	●							
Pipistrellus anchietai		●			●				
Pipistrellus kuhlii	●	●	●		●			●	
Pipistrellus nanus	●	●	●		●				
Rhinolophus blasii				●					
Rhinolophus clivosus		●	●	●		●	●	●	●
Rhinolophus darlingi			●				●		
Rhinolophus landeri		●					●		
Rhinolophus simulator	●	●	●	●	●				
Rhinolophus swinnyi			●				●		
Rousettus aegyptiacus	●	●	●	●					
Scotophilus borbonicus	●	●	●	●					●
Scotophilus dinganii	●	●	●	●		●			
Tadarida aegyptiaca	●	●	●		●	●		●	
Tadarida ansorgei			●						
Tadarida condylura	●	●	●		●				
Tadarida pumila	●		●	●					
Taphozous mauritianus	●	●	●	●	●				
Hyracoidea									
Dendrohyrax arboreus	●				●				
Procavia capensis	●	●	●	●	●	●	●	●	●
Insectivora									
Amblysomus hottentotus	●	●	●	●	●	●	●	●	●
Amblysomus marleyi			●						
Calcochloris obtusirostris	●		●						
Chlorotalpha sclateri								●	
Chrysospalax villosus		●			●				
Crocidura cyanea	●	●	●	●	●		●	●	
Crocidura flavescens	●	●	●	●	●	●		●	●
Crocidura hirta	●	●	●						
Crocidura fuscomurina	●	●	●						
Crocidura maquassiensis					●			●	
Crocidura mariquensis	●	●			●	●		●	
Crocidura silacea	●		●			●			●
Myosorex cafer	●	●	●		●				
Myosorex sclateri	●	●	●						
Myosorex varius	●	●	●	●	●	●	●	●	●
Suncus infinitesimus	●	●	●	●	●		●	●	
Suncus lixus	●	●	●	●					
Suncus varilla	●	●	●	●	●	●	●	●	
Lagomorpha									
Lepus saxatilis	●	●	●	●	●	●	●	●	●
Pronolagus crassicaudatus	●	●	●	●	●	●	●	●	●
Pronolagus rupestris						●	●	●	

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	CL	CH	LV	VB	MB	MU	DU	HL	MT
Macroscelidea									
Elaphantulus myurus				●			●		
Petrodromus tetradactylus	●		●						
Perissodactyla									
Ceratotherium simum		○	●	○		○			
Diceros bicornis	●		●	○					
Equus burchellii	●	○	●	○	○	○	○	○	
Pholidota									
Manis temminckii	●		●						
Primates									
Cercopithecus aethiops	●	●	●	●	●	●	●		
Cercopithecus mitis	●		●	●	●				
Otolemur crassicaudatus	●		●	●	●				
Papio ursinus	●		●	●			●	●	●
Proboscidea									
Loxodonta africana	●		●						
Rodentia									
Aethomys chrysophilus	●	●	●	●			●		
Aethomys namaquensis	●	●	●	●			●		
Cryptomys hottentotus	●	●	●	●	●	●	●	●	●
Dasymys incomtus	●	●		●	●	●		●	●
Dendromus melanotis	●		●			●		●	●
Dendromus mesomelas	●	●	●	●		●		●	●
Dendromus mystacalis	●	●	●	●	●	●		●	
Georychus capensis								●	●
Grammomys cometes	●		●				●	●	
Grammomys dolichurus	●	●	●	●	●				●
Graphiurus murinus	●	●	●	●	●	●	●	●	●
Hystrix africaeaustralis	●	●	●	●	●	●	●	●	●
Lemniscomys rosalia	●	●	●	●			●		
Mastomys natalensis	●	●	●	●	●	●	●	●	●
Mus minutoides	●	●	●	●	●	●	●	●	●
Mystromys albicaudatus						●	●	●	●
Otomys angoniensis	●	●	●	●	●	●	●		
Otomys irroratus	●	●	●	●	●	●	●	●	●
Otomys laminatus	●	●			●			●	
Otomys sloggetti								●	●
Paraxerus palliatus	●		●						
Pedetes capensis							●		
Rhabdomys pumilio	●	●	●	●	●	●	●	●	●
Saccostomus campestris	●		●	●			●		
Steatomys krebsii	●		●			●			
Steatomys pratensis	●		●					●	
Tatera brantsii	●		●	●			●	●	
Tatera leucogaster	●		●						
Thallomys paedulcus	●		●	●			●		
Thryonomys swinderianus	●	●	●	●	●	●		●	
Tubulidentata									
Orycteropus afer	●	●	●	●	●	●	●	●	