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THE RODENTS AND OTHER SMALL MAMMALS OF THE KALAHARI GEMSBOK NATIONAL PARK

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Abstract – The state of knowledge pertaining to the biology of small mammals occurring in the Kalahari Gemsbok National Park is reviewed with reference to completed and ongoing projects. Aspects of daily activity rhythms, habitat selection, diet, population fluctuations and changes in community structure, as well as reproduction are discussed. The zoogeography of the park is alluded to, and aspects which need additional attention are mentioned.

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Introduction

Free living small mammals are diverse groups of species which, by virtue of their abundance, practically universal distribution and wide ecological adaptations, are important components of nearly every existing terrestrial ecosystem. As Delany (1974) points out, their relationship to man is unfortunately only demonstrated when they become serious agricultural pests or vectors of diseases.

Research on small mammals in the Kalahari Gemsbok National Park (KGNP) ed with basic survey work during 1957/58, with sporadic trapping and observations during 1963, 1965, 1967/68 and censusing of specific habitats in 1967. Since 1970 an intensive survey of habitat selection by rodents (Nel & Rautenbach 1975; Nel 1978), community structure and long-term changes thereof (Nel & Rautenbach 1975; Nel 1978) and changes in population densities (Nel 1978, 1983) have been undertaken. Other aspects also received attention: post-natal development (Nel & Stutterheim 1973; Stutterheim & Skinner 1973); trap efficacy in capturing rodents (Nel & Rautenbach 1976); food utilized (Nel & Rautenbach 1974; Nel 1978); hoarding by some species (Nel 1967; Pettifer & Nel 1977); burrow systems (De Graaff & Nel 1965; Nel 1967); activity cycles of some species (*e.g. Parotomys brantsii* — Nel & Rautenbach 1974; Nel 1978); breeding (Skinner, Nel & Millar 1977); social ethology (Nel 1975b); while some species have come in for more detailed investigation, *e.g. Zelotomys woosnami* (Birkenstock & Nel 1977), *Thallomys paedulcus* (De Graaff 1978) and *Cryptomys hottentotus* (De Graaff 1972). Rodents as a food source for owls have also been investigated (Nel & Nolte 1965; Nel *in prep.*) while the small mammal fauna as a whole have been described by Davis (1958), Meester (1968), Rautenbach (1971), Rautenbach & Nel (1975), Schlitter & Rautenbach (1977), Erasmus & Rautenbach (1984).

Although research on most of the aspects mentioned above is still continuing, with some facets receiving in depth study, the present paper summarizes data accumulated so far and compares the rodent fauna of the southern Kalahari with that of other adjoining areas.

Study area

The results reported below were obtained in the KGNP, an area of some 9 453 km^2 in the semi-arid southern Kalahari system, which forms part of the South West Arid biotic zone. The mean altitude is *ca* 1 000 m a.s.l. and average annual rainfall varies from $\bar{x}$=220 mm p.a. in the south (Twee Rivieren) to $\bar{x}$=250 mm p.a. in the north around Nossob Camp, with large fluctuations from year to year.

Two main habitat types are here recognized: the undulating duneveld, and the usually dry rivercourses. Soil types in the park have been described by Louw (1964), Leistner (1967) and Van Rooyen (this volume). Vegetation has been discussed by Leistner (1967), Van Rooyen, Van Rensburg, Theron & Bothma (this volume), plant communities by Leistner & Werger (1973), and habitats by Bothma & De Graaff (1973).

In the park four areas were initially selected for a more detailed study of small mammal ecology: the dune area in the southern portion, the calcrete riverbanks (also in the south), the *Acacia* savanna in the north, and the riverbed also in the north (see Nel & Rautenbach 1975 for a detailed description). From 1980 a dune area west of Nossob Camp and close to the riverbed sampling area was also used; these two are *ca* three kilometres apart.

Methods

The survey of the small mammal fauna was initiated during 1958, and since then the conventional array of trapping and mistnetting techniques were employed (Smithers 1971; Nel & Rautenbach 1975; Rautenbach 1982). Lately macro-mistnets were employed (Rautenbach *in prep.*), which yielded unexpected new records of occurrences (see Erasmus & Rautenbach 1984).

Censusing of small mammal (predominantly rodents) densities and assessments of habitat selection was done by means of census lines. From 1970 to 1974 the dune and calcrete study sites in the south were sampled as was the *Acacia* savanna from 1971 to 1973, and again from 1980 onwards; the riverbed has been continuously sampled since 1970 (except in 1977 and 1979). Census lines in the dune area in the south consisted of 31 trap stations, 20 m apart; of 20 stations on the calcrete riverbank and *Acacia* savanna; and of 37 stations transversely through the riverbed. Since 1980 a trapline of 26 stations, again 20 m apart, sampled the dune area near the riverbed transect. At each trap station three traps, a Museum Special snap trap, a Victor rat and an aluminium Sherman live trap were set for three days and four nights, and baited with a mixture of rolled oats, peanut butter, golden syrup and sunflower oil. Traps were checked, rebaited and reset if necessary, early each morning and late afternoons. From 1970 to 1974 trapping sessions were normally six months apart; thereafter once yearly censuses (usually in summer) took place (see also Nel 1978, 1983). Occasional trapping away from census lines was also conducted (*e.g.* for *Parotomys brantsii* and *Thallomys paedulcus*) and trapping results were supplemented by sight records (*e.g. Pedetes capensis* and *Xerus inauris*). Trapped specimens were brought to the laboratory and sexed, weighed and measured, stomach contents analyzed and reproductive conditions noted.

To obtain an indication of their reproductive status males were examined externally and assigned to one of three categories based on the position and size of the testis: abdominal (no testes in scrotum), descended (testes present in scrotum but not enlarged), and developed (testes descended and enlarged). Females were also examined externally to determine whether they were lactating (milk present in the mammary glands) and/or perforated (vaginal orifice closed/not closed by an external membrane). The abdominal cavities of females were then opened to determine whether they were visibly pregnant or not. The number of embryos in each of the uterine horns were noted. In this study descended and enlarged testes in males as well as visible pregnancies, lactation or vaginal perforations of macroscopically non-gravid females are considered indicators of reproductive activity.

Reproductive tracts of 31 *Gerbillurus paeba* females (of which 11 were collected during January 1981, 14 during April 1981 and a further 6 during January 1983) were fixed in either Bouin's or AFA. These tracts were subsequently processed for histological examinations. Five micron serial sections were cut and every fifth section was mounted and stained with either haematoxylin and eosin or Mason's trichrome technique. The slides were used to determine early pregnancy (*i.e.* not visible macroscopically).

Rautenbach's (1978) numerical analyses of the credibility of the formerly empirically derived southern African biotic zones, have been reappraised based on an updated list of terrestrial mammal species occurring in each of the biotic zones. This list has been updated from published and unpublished records that became available since 1978, notably Smithers & Wilson (1979), Swanepoel, Smithers & Rautenbach (1980), Lynch (1983), Smithers (1983), Herselman & Norton (*in press*), Erasmus & Rautenbach (1984) and Meester, Rautenbach & Dippenaar (*in prep.*).

Results and discussions

At present 17 species of rodents are known to occur in the KGNP; of these 14 have been trapped (Table 1). In size these range from *ca* 5 g (*Mus minutoides*) to *ca* 3 kg (*Pedetes capensis*), with the majority (13 species) being less than 100 g in mass. It has been shown (Nel & Rautenbach 1976) that for capturing the smaller (<40 g) species Museum Special traps were most effective, for species weighing 40–60 g Museum Specials and Victor/McGill snap traps were equally effective, while for the larger species (>60 g) Victor/McGill and Sherman live traps were on par. Rodent moles (*Cryptomys hottentotus*) were captured with special tubular live traps. The use of pitfall traps has been sporadic and no species not captured in other kinds of traps have been captured in them. Although we are moderately confident that present data reflect the complete spectrum of small mammals present, a limited number of species may in future still be recorded for the first time. Some species may be present but as yet unrecorded as a result of very low numbers, while others have only been recognized (*e.g. Gerbillurus vallinus*) on re-examination of specimens housed in the Transvaal Museum (Schlitter & Rautenbach 1977). Other species (*e.g. Parotomys littledalei* and *Graphiurus murinus*) occur near the borders of the KGNP (and the south-western Kalahari) and may in time be found to be present in the park itself, as especially the south-western portions have been poorly sampled. Employing improved mistnetting techniques, Erasmus & Rautenbach (1984) have for example unexpectedly recorded *Scotophilus dinganii* within in the park.

Activity rhythms

Most of the rodents (13 species) occurring in the KGNP are nocturnal (Table 1). Only three (one sciurid, one cricetid and one murid) are diurnal, though in the case of *Parotomys brantsii* and *Rhabdomys pumilio* activity can continue till after dark, especially on moonlit nights (trapping records, and analysis of owl pellets — Nel & Nolte 1965, unpublished data). Conversely, a few normally nocturnal rodents will on occasion remain active after daybreak (*e.g. Gerbillurus paeba*) while others, especially *Thallomys paedulcus*, will become active during the late afternoon in winter. The activity rhythm of *Cryptomys hottentotus* is unknown, although one was seen active above ground in bright sunlight at 09h30 during July 1984.

Table 1

Species of rodents occurring in the southern Kalahari — average mass and times of activity

	Average mass (g)	Main activity period
Sciuridae		
*Xerus inauris**	615[1]	diurnal
Cricetidae		
Gerbillurus paeba	26	nocturnal
Gerbillurus vallinus	35[1]	nocturnal
Desmodillus auricularis	46	nocturnal
Tatera brantsii	65	nocturnal
Parotomys brantsii	80	diurnal
Dendromus melanotis	6	nocturnal
Malacothrix typica	13	nocturnal
Saccostomus campestris	47	nocturnal
Muridae		
Rhabdomys pumilio	32	diurnal
Mus minutoides	5	nocturnal
Aethomys namaquensis	43	nocturnal
Zelotomys woosnami	62	nocturnal
Thallomys paedulcus	80	nocturnal
Pedetidae		
Pedetes capensis	2 980[1]	nocturnal
Hystricidae		
Hystrix africaeaustralis	12 626[1]	nocturnal
Bathyergidae		
Cryptomys hottentotus	126[1]	?

[1] From Smithers, 1983
* Sight records

Habitat selection

Previous publications (Nel & Rautenbach 1975; Nel 1978) have outlined spatial distribution of rodents in the KGNP. Subsequent records have slightly expanded on these (Table 2). Most species occur in the dune troughs and dune slopes, while few utilize the calcrete riverbeds and silt riverbeds or pans; only one species (*G. paeba*) is known to occur in loose sand on unstabilized dune crests. These ecological distribution patterns obviously reflect species' abilities to cope with microhabitat conditions, though which factor(s) play the major role are at present uncertain — soil texture, microclimate, shelter or food, or combinations of these. For some species consolidated sand or silt (*e.g. X. inauris, P. capensis*) play perhaps the major

Table 2

Rodent species occurring in various habitats in the Kalahari Gemsbok National Park

Species	Dune crest	Dune slope	Dune trough	Calcrete river bank	Silt river bed	Pans	Plateau in river loops	*Acacia* savanna
Xerus inauris	–	–	–	–	+	+	+	–
Gerbillurus paeba	+	+	+	+	+	?	+	+
G. vallinus	?	+	+	–	–	–	–	–
Desmodillus auricularis	–	+	+	+	+	?	+	+
Tatera brantsii	–	+	+	+	–	–	+	+
Parotomys brantsii	–	+	+	–	–	–	–	+
Dendromus melanotis	–	+	–	–	–	–	+	–
Malacothrix typica	–	–	–	+	–	?	+	–
Saccostomus campestris	–	+	+	–	–	–	+	+
Rhabdomys pumilio	–	+	+	+	+	?	+	+
Mus minutoides	–	+	+	–	+	?	+	+
Aethomys namaquensis	–	+	+	–	–	–	–	+
Zelotomys woosnami	–	–	+	–	–	–	+	+
*Thallomys paedulcus**	–	+	+	–	+	–	+	+
Pedetes capensis	–	–	–	–	+	+	+	+
Hystrix africaeaustralis	?	+	+	+	?	?	+	+
Cryptomys hottentotus	–	+	+	–	–	–	+	+

* Only where large *Acacia erioloba* trees are present
+ = present
– = absent

role in influencing local distribution, while others (*e.g. D. auricularis* and *M. typica*) occur only in sparsely vegetated areas where enhanced auditory ability seems to be the major factor influencing their occurrence or not.

As far as vertical distribution is concerned only one species (*T. paedulcus*) is arboreal, one (*R. pumilio*) scansorial, one (*C. hottentotus*) truly fossorial, while the rest all burrow, but forage terrestrially.

Habitat-niche overlap occurs to a greater or lesser extent between all species (Nel 1978).

Diet

Based on stomach analyses, diets of only some species (*G. paeba, D. auricularis, T. brantsii, R. pumilio, M. minutoides, S. campestris, Z. woosnami, C. hottentotus*) are known. Analyses were conducted only in winter and summer (June–July or January–February respectively).

Gerbillurus paeba took mostly seeds (between 70–80%), less green plant material (leaves — 20–44%) and during summer also insects (up to 20%). *D. auricularis* likewise subsisted primarily on seeds (up to 80% during some years), up to 40% leaves, and up to 45% insects (in summer).

T. brantsii utilized up to 95% seeds (February 1981), up to 60% leaves, and up to 16% insects (the last instance again in summer). On the other hand *R. pumilio* showed a greater predilection for leaves (up to 72%), but its diet varied greatly, with on occasion (February 1983) including up to 60% seeds, and only 20% each of leaves and insects, and up to 80% seeds during February 1981. *M. minutoides* was found to be primarily a seedeater, while on the two occasions when the diet of *S. campestris* was sampled (February 1981 and February 1983) its diet was composed of 80% seeds, 15% leaves and 5% insects, and 76% seeds and 24% insects, respectively.

Zelotomys woosnami are known to be flesh-eaters (Nel 1978) but during February 1982 diet consisted of 76% seeds, 17% insects and 7% leaves. The diet of *C. hottentotus* was only determined during February 1982, when it consisted of 36% green material, 60% white (presumably stems or tubers) and 40% insects or other invertebrates.

In general, while most species seem to vary their intake of green leaves or seeds according to availability, but showing long-term trends in preference for either seeds or leaves, insects seem to be taken when available especially during summer, and probably in numbers relative to their occurrence. For some species a large degree of food-niche overlap has been demonstrated (Nel 1978).

Hoarding of food stores only occur in *D. auricularis* and *C. hottentotus* (larder hoarding) as far as is at present known. Trapped specimens with seeds in cheek pouches indicate that it probably also occurs in *S. campestris* as was found in laboratory studies (Pettifer & Nel 1977).

Population fluctuations and changes in community structure

These aspects have been reported upon previously (Nel 1978, 1983) and will only be summarized here. Since December 1970 up till February 1984 major fluctua-

Table 3

Reproductive status of four of the more frequently trapped rodent species in the Kalahari Gemsbok National Park

		FEMALES			MALES		
Month	n	Gravid	Non-gravid	n	Abd.	Desc.	Dev.
G. paeba							
(n=624: 341 females + 283 males)							
Nov.	3	2	1	7	2	0	5
Dec.	1	0	1	2	0	0	2
Jan.	97	16	81	150	0	45	105
Febr.	60	26	34	17	0	10	7
April	12	9	3	0	—	—	—
May	32	0	32	27	5	6	16
July	136	0	136	80	24	24	32
R. pumilio							
(n=178: 66 females + 112 males)							
Nov.	7	0	7	19	0	1	18
Jan.	13	2	11	26	3	8	14
Febr.	0	—	—	2	0	0	2
May	38	0	8	7	0	1	6
July	38	0	38	58	48	5	5
T. brantsii							
(n=82: 48 females + 34 males)							
Nov.	3	2	1	6	0	0	6
Jan.	19	2	17	15	0	1	14
May	1	0	1	1	0	0	1
July	25	2	23	12	0	0	12
D. auricularis							
(n=61: 36 females + 25 males)							
Nov.	2	0	2	1	0	1	0
Jan.	15	1	14	12	0	10	2
Febr.	1	0	1	0	—	—	—
May	2	0	0	1	1	0	0
July	16	0	16	11	3	5	3

n = sample size; Abd. = testes abdominal; Desc. = testes descended; Dev. = testes developed.

tions have occurred in population sizes of trapped rodents in the KGNP, although only two species (*G. paeba* and *R. pumilio*) normally occur in great enough numbers to allow year to year comparisons of fluctuations.

Total rodent numbers, or those of particular species, track increased rainfall closely with gradual build-up, but abrupt declines. Also, not all species undergo population changes of similar magnitude (Nel 1983). In some cases especially, increased seed production seems to be the principal factor involved in allowing increase in numbers (*e.g. G. paeba*), while in others enhanced cover coupled to increased food production create favourable circumstances for population increase (*e.g. R. pumilio*).

Similarly, and in conjunction with the population fluctuation of the different species, changes in community structure of especially the riverbed and dune communities occur (Nel 1978). Over the years only two species have been consistently very numerous (*G. paeba* and *R. pumilio*) with *G. paeba* being the dominant species in most years, with *R. pumilio* usually dominant only in winter (*e.g.* July of 1974, 1975 and 1976).

Reproduction

Only macroscopically non-gravid *G. paeba* (168) were collected during May and July (Table 3). Six per cent (10) of these females had perforated vaginae. Of the macroscopically non-gravid females (120) collected during the warmer months 53% (64) had non-perforated vaginae indicating no reproductive activity whatsoever. Of all the females (173) accrued during the summer months 64% (111) showed some form of reproductive activity (31% (53) were gravid, 1% (2) of the non-gravid females were lactating and 32% (56) had perforated vaginae). Hence, considerably more reproductive activity was observed during the warmer than the colder months. Gravid animals were only collected during summer while lactation was recorded during most of the months that material was collected, probably suggesting inordinately long lactation periods during autumn and winter. Litter size of *G. paeba* was $\bar{x}=4{,}1$ ($n=20$) and no predilection for any side of uterine implantation was observed (left uterine horn $\bar{x}=2{,}1$; right uterine horn $\bar{x}=2{,}0$). Using descended and well developed testes as an indicator of reproductive activity in males, the obtained information (Table 3) shows sexual activity throughout the year: 73% were active during colder months and 99% during warmer months.

Based on macroscopical examination *G. paeba* in the KGNP thus display a marked decrease in reproductive potential during winter, in accordance with laboratory observations by Keogh & Isaacson (1978). However, though no litters were recorded during winter in the KGNP, the ability of this species to reproduce during winter months is demonstrated by the observations of Smithers (1971, 1983) in Botswana.

The microscopical examination of the reproductive tracts of the 31 *G. paeba* females collected during January and April 1981 as well as January 1983, revealed 26 animals to be gravid. Only 18 of these were macroscopically pregnant. The eight females whose pregnancies could only be established microscopically, constitute a significant reconsideration in the interpretations of macroscopical investigations.

Since similar microscopical examinations were not conducted on material accrued during winter, it is impossible to ascertain the true incidence of gravidity during winter. Considering the higher incidence of pregnancy obtained through microscopical examination of *G. paeba*, it is evident that the actual occurrence of pregnancy in all of the studied genera are probably of a higher order than reflected by the data in Table 3. In ongoing studies of the reproduction cycles of KGNP small mammals, all female reproductive tracts will be microscopically examined.

Though a relatively small sample of *Rhabdomys pumilio* females were collected during summer months (20), including only one gravid female (Table 3), more of these animals (35%) (7) had perforated vaginae than those collected during May and July. Only one litter size was recorded from a gravid female with seven embryos (three in the left and four in the right uterine horn). Of the males collected during November, January and February 91% (43) had descended or well developed testes as compared with 26% (17) for those collected during May and July. These results appear to correspond with breeding patterns in Zimbabwe (Smithers & Wilson 1979), Transvaal (Brooks 1974) and the plains of the South-west Cape (Henschel, David & Jarvis 1981). In Botswana pregnancies for this species was recorded during summer as well as winter months (Smithers 1971, 1975). The latter corresponds with the laboratory results of Brooks (1974).

Gravid *T. brantsii* females constituted 18% (4) of the summer recordings (November and January) and 8% (2) of the winter collections (May and July), while lactation was recorded during most of the months covered (Table 3). Fewer non-gravid animals showed vaginal perforations during winter than summer months. An average litter size of 3,2 (n=6) was observed from an investigation of gravid animals ($\bar{x}$=2,0 embryos in the left and $\bar{x}$=1,2 in the right uterine horn). Males consistently had well developed testes. The reproductive activity of *T. brantsii* in the KGNP coupled to Smithers' (1971) and Measroch's (1954) findings in Botswana suggest breeding throughout the year.

From the information on the occurrence of gravid and lactating animals together with the incidence of vaginal perforations and the testicular development (Table 3) it seems likely that *D. auricularis* could breed throughout the year, albeit at a decreased rate during winter. The only gravid animal was collected during summer, which had two embryos (both in the right uterine horn). Though food availability probably exerts a strong influence on breeding seasonality, it is important to note that Keogh (1972) as well as Keogh & Isaacson (1978) had to lengthen the daily light cycle under laboratory conditions before breeding activities commenced. According to Smithers (1983) this species breeds throughout the year in Botswana.

Though very little information was obtained on the reproductive status of less common rodent species, lactation was recorded for *M. minutoides* during July and a pregnant *Z. woosnami* was collected during winter. With reference to the parameters used as indicators of reproductive activity, the material obtained for *P. brantsii, D. melanotis, S. campestris, A. namaquensis* and *T. paedulcus* provide some indication of higher reproductive activity during the warmer wet months. These observations for the KGNP are in accordance with recorded breeding patterns for these species by Smithers (1971), Swanepoel (1972), and De Graaff

(1981). A gravid *A. namaquensis* collected in February had five embryos (four in the left and one in the right uterine horn).

The KGNP mammalian fauna in comparison with those of other biomes

Rautenbach (1978) mathematically analysed the credibility of the formerly empirically derived biotic zones of southern Africa. Six biogeographical entities, each with its distinctive faunal composition and endemic species, are recognized. The South West Arid zone is by far the largest of the biotic zones, but with only the second largest species richness: a total of 133 currently being recognized. The species known to occur in the KGNP are marked with asterisks in Table 4. The list of southern African terrestrial mammalian species and their occurrences in the six biotic zones recognized, is an updated version of the list given by Rautenbach (1978). Although this list differs in some detail from the previous one, the conclusions drawn from the 1978 list, are still valid when calculated from the information contained in the current list.

The KGNP falls well within the confines of the South West Arid biotic zone. A total of 59 mammal species are known to occur in the KGNP. The question arises as to why the species richness of the KGNP is so depauperate when compared with that of the South West Arid biotic zone as a whole. The relative restricted areal size of the KGNP is the first reason that springs to mind. The majority of the species that constitute the distinctive faunal composition of a particular biotic zone, do not range throughout that particular zone, thus no sub-division of any biotic zone could exhibit a species richness comparable to that of the biotic zone itself. This phenomenon is obviously correlated with the dispersal abilities of individual species, which in turn is related to the ecological diversity of a particular region.

With the information at hand, we propose that the comparatively low mammalian species richness of the KGNP can, to a large extent, be attributed to restricted ecological diversification, thus precluding species with particular habitat requirements to extend their geographical ranges to within the boundaries of the park. Rupiculous species adapted to arid environments such as *Acomys subspinosus, Petromyscus collinus, Sauromys petrophilus, Pronolagus rupestris, Graphiurus platyops* and *G. ocularis* are all precluded from the KGNP as the result of the absence of mountains with associated rocky habitats. The lack of permanent open water sources and related semi-aquatic water vegetation, likewise precludes a host of species that could potentially occur in the area under discussion, including a number of *Crocidura* species, the two otter species (*Aonyx* and *Lutra*), *Otomys irroratus, O. angoniensis, Genetta tigrina, Praomys natalensis, P. coucha* and others. Although aardvark holes provide daytime roosts for at least one species of bat, it is postulated that the presence of caves and equivalent structures serving as daytime roosts, would allow more species of cave bats to range to within the park.

Low ecological diversity within the park could also preclude a number of species from occurring in the park, for as yet unresolved reasons. Seemingly the KGNP offers suitable habitat to the following small mammal species which are absent: *Paraxerus cepapi, Graphiurus murinus, Parotomys littledalei, Lepus saxatilis* and *Galago senegalensis*.

On the other hand the species diversity in the KGNP has been found to be unexpectedly high (Nel 1975).

Table 4

Breakdown of the terrestrial mammal species occurring in the different regions of southern Africa (exotic species excluded, but extinct species included). The 59 species known to occur in the Kalahari Gemsbok National Park are marked with an asterisk

Symbols: X = present; — = absent in particular zoogeographic region.

	Namib	SWA	SWC	SSW	SSG	FOREST
Myosorex longicaudatus	—	—	X	—	—	X
M. cafer	—	—	—	X	X	X
M. varius	—	X	X	X	X	X
Suncus lixus	—	—	—	X	—	—
S. varilla	—	X	X	X	X	—
S. infinitesimus	—	—	X	X	X	—
Crocidura mariquensis	—	—	—	X	X	—
C. bicolor	—	X	—	X	X	—
C. maquassiensis	—	—	—	X	X	—
C. cyanea	X	X	X	X	X	X
C. gracilipes	—	—	—	X	X	—
C. flavescens	—	—	X	X	X	X
C. luna	—	—	—	—	—	X
**C. hirta*	—	X	—	X	X	X
Sylvisorex megalura	—	—	—	X	—	X
**Erinaceus frontalis*	—	X	—	X	X	—
Chrysospalax trevelyani	—	—	—	X	—	X
C. villosus	—	—	—	X	X	X
Cryptochloris wintoni	—	X	—	—	—	—

Table 4 (cont.)

	Namib	SWA	SWC	SSW	SSG	FOREST
C. zyli	—	X	—	—	—	—
**Chrysochloris asiatica*	—	X	X	—	—	—
C. visagiei	—	X	—	—	—	—
Eremitalpa granti	X	X	X	—	—	—
Chlorotalpa arendsi	—	—	—	—	—	X
C. duthiae	—	—	X	—	—	—
C. sclateri	—	X	—	—	X	—
Calcochloris obtusirostris	—	—	—	X	—	—
Amblysomus gunningi	—	—	—	—	—	X
A. iris	—	—	X	X	X	—
A. hottentotus	—	—	X	X	X	X
A. julianae	—	—	—	X	X	—
Petrodromus tetradactylus	—	—	—	X	—	X
**Macroscelides proboscideus*	X	X	—	—	—	—
Elephantulus fuscus	—	—	—	X	—	—
E. brachyrhynchus	—	—	—	X	X	—
E. rupestris	—	X	X	—	—	—
**E. intufi*	X	X	—	X	—	—
E. myurus	—	—	—	X	X	—
E. edwardi	—	X	X	—	—	—
Epomophorus wahlbergi	—	—	X	X	—	X
E. angolensis	—	—	—	X	—	—
E. gambianus	—	—	—	X	—	—
E. crypturus	—	—	—	X	—	—
Epomops dobsoni	—	—	—	X	—	—

Table 4 (cont.)

	Namib	SWA	SWC	SSW	SSG	FOREST
Eidolon helvum	—	X	—	X	X	—
Rousettus aegyptiacus	—	—	X	X	—	X
R. angolensis	—	—	—	—	—	X
Coleura afra	—	—	—	X	—	—
Taphozous mauritianus	—	X	X	X	X	—
T. perforatus	—	—	—	X	—	—
Otomops martiensseni	—	—	—	X	—	—
Sauromus petrophilus	X	X	X	X	—	—
Tadarida acetabulosa	—	—	—	X	—	—
T. midas	—	—	—	X	—	—
T. condylura	—	—	—	X	—	X
T. nigeriae	—	—	—	X	—	—
T. bivittata	—	—	—	X	—	—
T. chapini	—	—	—	X	—	—
T. pumila	—	X	X	X	—	—
T. lobata	—	—	—	X	—	—
T. ventralis	—	—	—	X	—	—
T. fulminans	—	—	—	X	—	—
**T. aegyptiaca*	—	X	X	X	X	X
T. ansorgei	—	—	—	X	—	—
Miniopterus inflatus	—	—	—	X	—	—
M. fraterculus	—	—	X	X	—	—
M. schreibersii	X	X	X	X	X	X
Myotis welwitschii	—	—	—	X	X	—
M. seabrai	X	X	—	—	—	—

Table 4 (cont.)

	Namib	SWA	SWC	SSW	SSG	FOREST
M. leseuri	—	X	X	—	—	—
M. tricolor	—	—	X	X	X	—
M. bocagei	—	—	—	X	—	—
Pipistrellus kuhlii	—	—	—	X	X	X
P. rusticus	—	—	—	X	—	X
P. nanus	—	—	—	X	—	X
P. ruepellii	—	—	—	X	—	—
Chalinolobus variegatus	—	—	—	X	—	—
Laephotis namibensis	X	—	—	—	—	—
L. botswanae	—	—	—	X	—	—
L. wintoni	—	—	X	—	—	—
Eptesicus rendalli	—	—	—	X	—	—
E. hottentotus	X	X	X	X	—	—
E. melckorum	—	X	X	—	—	—
E. zuluensis	—	—	—	X	—	—
E. somalicus	—	—	—	X	—	—
**E. capensis*	X	X	X	X	X	—
Scotophilus nigrita	—	—	—	X	—	—
**S. dinganii*	—	X	—	X	—	—
S. viridis	—	—	—	X	—	—
Nycticeius schlieffenii	—	—	—	X	—	—
Scotocus albofuscus	—	—	—	X	—	—
Kerivoula argentata	—	—	—	X	—	—
K. lanosa	—	—	X	X	—	—
Nycteris hispida	—	—	—	X	—	X

Table 4 (cont.)

	Namib	SWA	SWC	SSW	SSG	FOREST
N. grandis	—	—	—	X	—	X
N. woodi	—	—	—	X	—	X
N. macrotis	—	—	—	X	—	X
**N. thebaica*	X	X	X	X	X	X
N. vinsoni	—	—	—	X	—	—
Rhinolophus hildebrantii	—	—	—	X	—	X
R. fumigatus	—	X	—	X	—	—
R. clivosus	—	X	X	X	X	X
R. darlingi	—	X	—	X	—	—
R. landeri	—	—	—	X	—	—
R. blasii	—	—	—	X	—	—
R. capensis	—	X	X	X	—	—
R. simulator	—	—	—	X	—	—
R. denti	—	X	—	X	—	—
R. swinnyi	—	—	—	X	—	—
Hipposideros commersoni	—	X	—	X	—	—
H. caffer	—	X	—	X	—	X
Cloeotis percivali	—	—	—	X	—	—
Triaenops persicus	—	—	—	X	—	—
Galago crassicaudatus	—	—	—	X	—	X
G. senegalensis	—	—	—	X	—	X
G. moholi	—	—	—	X	—	—
**Papio ursinus*	—	X	X	X	X	X
P. cynocephalus	—	—	—	X	—	—
**Cercopithecus pygerythrus*	—	X	X	X	X	X

Table 4 (cont.)

	Namib	SWA	SWC	SSW	SSG	FOREST
C. albogularis	—	—	—	X	—	X
**Manis temminckii*	—	X	—	X	X	—
**Lepus capensis*	X	X	X	X	X	—
L. saxatilis	—	X	X	X	X	—
Pronolagus rupestris	—	X	X	—	X	—
P. crassicaudatus	—	—	—	X	X	—
P. randensis	—	X	—	X	X	—
Bunolagus monticularis	—	X	—	—	—	—
Bathyergus suillus	—	—	X	—	—	X
B. janetta	—	X	—	—	—	—
Heliophobius argenteocinereus	—	—	—	X	—	—
**Cryptomys hottentotus*	—	X	X	X	X	X
Georhychus capensis	—	—	X	—	X	—
**Hystrix africaeaustralis*	X	X	X	X	X	X
**Pedetes capensis*	X	X	—	X	X	—
Graphiurus ocularis	—	X	X	—	—	—
G. platyops	—	X	—	X	X	—
G. murinus	—	X	X	X	X	X
G. parvus	—	—	—	X	—	—
**Xerus inauris*	—	X	—	—	X	—
X. princeps	—	X	—	—	—	—
Heliosciurus rufobrachium	—	—	—	X	—	X
Funisciurus congicus	—	—	—	X	—	—
Paraxerus palliatus	—	—	—	—	—	X
P. cepapi	—	—	—	X	—	—

Table 4 (cont.)

	Namib	SWA	SWC	SSW	SSG	FOREST
Thryonomys swinderianus	—	—	—	X	—	—
T. gregorianus	—	—	—	X	—	—
Petromus typicus	X	X	—	—	—	—
**Parotomys brantsii*	X	X	X	—	—	—
P. littledalei	X	X	—	—	—	—
Otomys laminatus	—	—	—	X	X	X
O. angoniensis	—	X	—	X	X	—
O. maximus	—	—	—	X	—	—
O. saundersiae	—	—	X	X	X	—
O. irroratus	—	X	X	X	X	X
O. sloggetti	—	—	—	—	X	—
O. unisulcatus	—	X	X	—	—	—
Pelomys fallax	—	—	—	X	—	X
Acomys spinossissimus	—	—	—	X	—	X
A. subspinosus	—	—	X	—	—	X
Lemniscomys griselda	—	X	—	X	—	—
**Rhabdomys pumilio*	X	X	X	X	X	X
**Zelotomys woosnami*	—	X	—	—	—	—
Dasymus incomtus	—	—	X	X	X	—
Thamnomys cometes	—	—	—	—	—	X
T. dolichurus	—	—	—	X	—	X
Mus setzeri	—	X	—	X	—	—
M. triton	—	—	—	X	—	—
M. industus	—	X	—	X	—	—
**M. minutoides*	—	X	X	X	X	X

Table 4 (cont.)

	Namib	SWA	SWC	SSW	SSG	FOREST
Uranomys ruddi	—	—	—	X	—	—
Praomys natalensis	—	X	X	X	X	X
P. shortridgei	—	—	—	X	—	—
P. verreauxii	—	—	X	—	—	X
**Thallomys paedulcus*	X	X	—	X	—	—
Aethomys silindensis	—	—	—	—	—	X
**A. namaquensis*	X	X	X	X	X	—
A. granti	—	X	—	—	—	—
A. chrysophilus	—	X	—	X	X	—
A. nyikae	—	—	—	—	—	X
**Desmodillus auricularis*	X	X	X	X	X	—
**Gerbillurus paeba*	X	X	X	X	—	—
G. tytonis	X	—	—	—	—	—
**G. vallinus*	X	X	—	—	—	—
G. setzeri	X	—	—	—	—	—
Tatera leucogaster	X	X	—	X	X	—
T. afra	—	—	X	—	—	—
**T. brantsii*	—	X	—	X	X	—
T. inclusa	—	—	—	X	—	—
Mystromys albicaudatus	—	—	X	—	X	—
Cricetomys gambianus	—	—	—	X	—	X
**Saccostomus campestris*	—	X	X	X	X	—
**Malacothrix typica*	—	X	—	—	X	—
Dendromus nyikae	—	—	—	—	—	X
**D. melanotis*	—	X	X	X	X	X

Table 4 (cont.)

	Namib	SWA	SWC	SSW	SSG	FOREST
D. mesomelas	—	—	X	X	X	X
D. mysticalis	—	—	X	X	X	X
Steatomys pratensis	—	X	—	X	—	—
S. parvus	—	X	—	X	X	—
S. krebsii	—	X	X	X	X	—
Petromyscus monticularis	—	X	—	—	—	—
P. collinus	X	X	—	—	—	—
**Proteles cristatus*	X	X	X	X	X	—
**Hyaena brunnea*	X	X	—	X	X	—
**Crocuta crocuta*	X	X	—	X	X	—
**Acinonyx jubatus*	—	X	—	X	—	—
**Panthera pardus*	X	X	X	X	X	X
**P. leo*	—	X	X	X	X	—
**Felis caracal*	X	X	X	X	X	—
**F. lybica*	X	X	X	X	X	—
**F. nigripes*	—	X	—	—	X	—
F. serval	—	—	—	X	X	—
**Otocyon megalotis*	X	X	X	X	X	—
**Lycaon pictus*	—	X	—	X	—	—
**Vulpes chama*	X	X	X	X	X	—
Canis adustus	—	—	—	X	—	—
**C. mesomelas*	X	X	X	X	X	—
Aonyx capensis	—	X	X	X	X	—
Lutra maculicollis	—	X	X	X	X	—
**Mellivora capensis*	—	X	X	X	X	—

Table 4 (cont.)

	Namib	SWA	SWC	SSW	SSG	FOREST
Poecilogale albinucha	—	X	X	X	X	—
**Ictonyx striatus*	X	X	X	X	X	—
Nandinia binotata	—	—	—	—	—	X
Civettictis civetta	—	—	—	X	—	—
**Genetta genetta*	X	X	X	X	X	—
G. tigrina	—	—	X	X	X	X
**Suricata suricatta*	X	X	—	—	X	—
Paracynictis selousi	—	—	—	X	—	—
Bdeogale crassicauda	—	—	—	X	—	—
**Cynictis penicillata*	—	X	X	X	X	—
Herpestes ichneumon	—	—	X	X	—	—
**Galerella sanguinea*	—	X	—	X	X	X
G. pulverulenta	—	X	X	—	X	—
Rhynchogale melleri	—	—	—	X	—	X
Ichneumia albicauda	—	—	—	X	X	X
Atilax paludinosus	—	X	X	X	X	X
**Mungos mungo*	—	X	—	X	—	—
Helogale parvula	—	—	—	X	—	—
**Orycteropus afer*	—	X	X	X	X	—
Loxodonta africana	—	X	—	X	X	X
Procavia capensis	X	X	X	X	X	X
P. welwitchii	X	X	—	—	—	—
Heterohyrax brucei	—	—	—	X	—	—
Dendrohyrax arboreus	—	—	—	X	—	X
Ceratotherium simum	—	X	—	X	X	—

Table 4 (cont.)

	Namib	SWA	SWC	SSW	SSG	FOREST
Diceros bicornis	—	X	X	X	—	—
Equus zebra	X	X	—	—	—	—
E. burchelli	—	X	—	X	X	—
E. quagga	—	X	X	—	—	—
Potamochoerus porcus	—	—	X	X	—	X
Phacochoerus aethiopicus	—	X	—	X	—	—
Hippopotamus amphibius	—	X	X	X	X	—
Giraffa camelopardalis	—	X	—	X	—	—
Connochaetes gnou	—	X	—	—	X	—
**C. taurinus*	—	X	—	X	X	—
Alcelaphus lichtensteinii	—	—	—	X	—	—
**A. buselaphus*	—	X	—	X	—	—
Damaliscus dorcas	—	X	X	—	X	—
D. lunatus	—	—	—	X	—	—
Cephalophus monticola	—	—	—	X	—	X
C. natalensis	—	—	—	X	—	X
**Sylvicapra grimmia*	X	X	X	X	X	—
**Antidorcas marsupialis*	X	X	—	—	X	—
Oreotragus oreotragus	—	X	X	X	X	—
Madoqua kirkii	—	X	—	—	—	—
Ourebia ourebi	—	—	—	X	X	—
**Raphicerus campestris*	—	X	X	X	X	—
R. melanotis	—	—	X	X	—	—
R. sharpei	—	—	—	X	—	—
Neotragus moschatus	—	—	—	X	—	—

Table 4 (cont.)

	Namib	SWA	SWC	SSW	SSG	FOREST
Aepyceros melampus	—	—	—	X	—	—
Pelea capreolus	—	X	X	X	X	—
Hippotragus equinus	—	—	—	X	—	—
H. leucophaeus	—	—	X	—	—	—
H. niger	—	—	—	X	—	—
**Oryx gazella*	X	X	—	X	—	—
Syncerus caffer	—	—	—	X	—	—
**Tragelaphus strepsiceros*	—	X	X	X	—	—
T. spekei	—	—	—	X	—	—
T. angasii	—	—	—	X	—	—
T. scriptus	—	—	X	X	—	—
**Taurotragus oryx*	—	X	—	X	X	—
Redunca arundinum	—	—	—	X	—	—
R. fulvorufula	—	—	X	X	X	—
Kobus ellipsiprymnus	—	—	—	X	—	—
K. leche	—	—	—	X	—	—
K. vardonii	—	—	—	X	—	—
SUBTOTALS	45	133	97	224	109	73

A total of 287 endemic subcontinental terrestrial mammalian species
SWA = South West Arid
SWC = South West Cape
SSW = Southern Savanna Woodland
SSG = Southern Savanna Grassland

Conclusions

The species listed in Table 4 as well as results from the research mentioned above form a basis from which additional in-depth research may be generated in this semi-arid and undisturbed ecosystem. It is not enough merely to know which species occur within the boundaries of the park. Future research on small mammals will be likely to be directed at (i) improved field methods which would lead to better estimations of home ranges, population densities and indices of abundance: (ii) more complete information on life histories and demography to elucidate reproductive cycles, breeding seasonality, information on litter size, post-natal development, population structure and survivorship: and (iii) more detailed information on populations as entities. The latter would lead to improved knowledge on population dynamics, population cycles, food supplies, effects of adverse environmental conditions (including droughts, floods, fires), intraspecific regulatory mechanisms as well as aspects of predation: and (iv) finally, the habitat exploitation by small mammal species promises exciting research prospects, especially as this may relate to range management potential. This would include aspects such as species diversity in different habitats, ecological distribution, activity patterns, interspecific competition and feeding habits (*e.g.* Nel 1978). A study of energy dynamics operating within populations on both inter- and intraspecific level, will be possible with more detailed information at hand, such as envisaged above.

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