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Small mammal diversity in Kalahari

— impact of land-use and pans in a semi-arid savanna,
southwestern Botswana



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*Seems so easy
Just to let it go on by
Till you stop and wonder
Why you never wondered why*

~

Savanna /S_ˈvæn_/_ n [C, U] a large flat area of grassy land in a warm part of the world
(Longman dictionary of contemporary english)

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1. Abstract

The aim of this study was to examine and determine variation in small mammal species diversity and abundance along the two types of gradients. The main hypothesis is that small mammal abundance and species diversity increases with increasing grass cover, thus increasing with lessened grazing impact as a result of decreasing human impact or with increasing distance from pans.

Savannas are the most widespread vegetation types in Africa and cover one fifth of the earth's land surface. They are therefore of big ecological significance for vegetation, animals and humans world wide, and hence an important subject of research. Human activities, such as cattle herding and growing crops are widespread in most savannas, and affect the ecosystem. The area concerned in this study is divided into different land use types, creating gradients in human activities, notably livestock grazing from the areas close to villages and settlements to relatively unexploited areas in the National Parks. Smaller scale gradients, enclosed in the landuse gradients, are connected to the variation in soil and vegetation with distance to pans. Pans are shallow depressions with sparse vegetation and saline, mineral rich soils occurring throughout the Kalahari savanna. They are of great importance as key habitats for wild large herbivores and provide high quality forage for herbivores. Hence, with increasing distance from pans, generally, grazing pressure of wild and/or domestic large herbivores as well as mineral content of the vegetation decreases.

The study was realized through selecting pans in areas with different landuse and distributing live-traps in a predefined pattern along a five kilometre transect reaching from the edge of the pan to savanna unaffected by the pan. The traps were in place for three consecutive days and the rodents captured were determined to species level measured and marked (as to be identified if recaptured). Along the transect various environmental parameters were measured or estimated.

The study indicates differences in grass cover and bush/tree cover both between the pans in the different land use types and within the transect reaching out from the pan. Abundance of small mammals increased, along with grass cover, with increasing distance until ca 2 km where the pan impact evens out and the landscape becomes more homogenous. On the larger scale, abundance of small mammals was highest in the national park, and seemed to decrease with increasing human and livestock impact. Vegetation cover seems to be an important factor for the abundance and diversity of small mammals presumably because it functions both as food supply and shelter, but probably other factors should be taken into account as well.

2. Introduction

2.1 Interaction between large herbivores and small mammals on the savanna

Savannas are the most widespread vegetation types in Africa and cover one fifth of the earth's land surface. They are therefore of big ecological significance for vegetation, animals and humans world wide, and hence an important subject of research. Due to an increasing number of people and an intensified exploitation, the savannas throughout the world are subjected to great changes. In the savannas of Botswana this is certainly the case (Perkins, 1991). In addition to the large natural variation in savanna ecosystems, cultivation, cutting of wood and increasing numbers of cattle, goats and sheep have great impact. Following large grazing impact the grass cover is reduced giving way to bush encroachment (Van Vegten 1983). As a result the carrying capacity for grazing large herbivores is reduced. As Adler et al. (2001) state it: "Changes in spatial heterogeneity caused by grazing imply changes in habitat diversity, and influence the diversity of consumers ranging from insects to birds and mammals". Studies on impacts on wild large herbivores by livestock grazing in Botswana (Bergström & Skarpe, 1999; Wallgren, 2001; Granlund, 2001, Viio 2003) suggest that cattle grazing causes a decline in number of both species and individuals of most wild mammals. This applies to larger wild animals, but less is known about effects on smaller mammals.

Concerning the number of species of small mammals and their distribution, quite a lot is known (Skinner & Smithers, 1990) in the study area, but less is known on habitat preference and utilization (Rudinow Saetnan, 2000; Nel & Rautenbach 1975). While large animals can be seen as regulators of savanna ecosystem processes (Hobbs, 1996), smaller animals may have equally important key functions as consumers of plant biomass (Keesing 2000), as predators on and distributors of seed (Ostfeld & Keesing 2000) and as prey animals for a number of other species (Linzey & Kesner 1997, Sejo, 1999) as well as for changing abiotic factors through burrowing and impact on nutrient recycling (Rudinow Saetnan, 2000). Another important role of small mammals in the ecosystem is their interaction with ungulates and vegetation (Keesing, 1998). This author shows that the density of small mammals may increase two-fold in the absence of ungulates and reduce the plant biomass by 40%. This suggests, although it could be debated, (Rudinow Saetnan, 2000) two things: that the large and the small herbivores may compete for the same food resources, which is the basis for this study's hypothesis, and that the small herbivores impose a large impact on its environment and are an important subject of research.

Small mammals can also be seen as indicators of environmental conditions (Linzey & Kesner, 1997), as changes in the environment, caused e.g. by drought or heavy grazing, lead to changes in the habitats for small mammals and quickly affect their abundance, survival and breeding success (Dooley & Bowers, 1996).

2.2 Gradients in land-use and resources

Traditional land use in the form of hunting and gathering may have had only negligible effects on the Kalahari savannas. Also, the heavy impact of traditional pastoralism was limited in extent, due to limited water availability. More recently, with the widespread drilling for water from about the 1960's, the impact has been more intense and more wide spread. There is a gradient in land use intensity and human impact from heavily impacted areas on livestock ranches and village

surroundings to little affected protected areas like national parks. Recent studies in the area indicate that there is indeed a disturbance gradient affecting both large herbivores (Granlund, 2001; Wallgren, 2001; Viio, 2003) and insect communities (Åström, 2003), although in different ways. Hypothetically, this gradient would also affect small mammals, as the disturbance include impact on food supply, vegetation cover, suitability of substrate for digging etc., all of which could be important factors for small mammal abundance and diversity.

On a landscape scale the semi-arid savannas of Botswana are fairly homogenous. However, spread throughout the landscape are the pans, i.e. shallow depressions with clayey saline soils and devoid of higher vegetation. The pans are of great importance as key habitats for wildlife in the Kalahari. The pan surroundings provide high quality mineral rich vegetation for herbivores, but a fairly low quantity of forage (Skarpe, 1986). The pans also provide mineral licks and temporary water supplies (Wallgren, 2001). The role of the pans as key habitats for wildlife is increasingly threatened by intensified cattle grazing and human exploitation.

The present study is concentrated on the gradient in land use intensity, and on the smaller scale gradients in resource availability with distance from pans, and on their interactions. Aava-Olsson (2001) refers to three hypotheses on the relationship between plant productivity and animal species richness which are of importance here. The first one, the "energy limitation" hypothesis states that the number of individuals that can be sustained in a habitat is dependent on the energy available in the area. The energy in its turn is dependent of plant productivity. When plant productivity increases, so will the number of consumer individuals and as a result the number of species. The second hypothesis, the "environmental heterogeneity" hypothesis states that when productivity is low the habitats can hold few species as low productivity render resources homogenous. The last hypothesis, the "more specialisation" hypothesis, states that rare resources will increase with increased plant productivity, enabling specialist species to thrive (Aava-Olsson, 2001).

The fact that soil-nutrient concentrations decrease gradually away from the pan, resulting in a decrease in forage quality and in grazing intensity by domestic and wild large herbivores, and possibly in plant productivity, could be important factors for the small mammals. Also the gradient in land use intensity may imply reduced plant productivity, at least of grasses and forbs, in the most intensely used areas, which may play an important role for the small mammal abundance and diversity. On the larger scale, the land use gradient includes the pan gradients (a resource gradient and a grazing gradient).

2.3 Rational

In this study I have examined how the gradients connected to the land use and to the pans affect species distribution and abundance of small mammals. The study was affiliated an EU-funded cooperation project between the countries of Botswana, Lesotho, Norway, South Africa, Spain and Wales called "Management and policy options for the sustainable development of communal rangelands and their communities in southern Africa" (MAPOSDA, Project No. ICA4-CT-2001-10050) with field work sites in the three African countries. The project is partly socio-economic (the largest part) and partly bio-physical. The two parts are closely integrated and is a result of the recognized need to maintain and increase the multifunctionality of the Kalahari rangelands. This includes subsistence hunting and gathering, livestock husbandry and arable agriculture, sustainable

harvesting of economically important plants, consumptive and non-consumptive tourism and, in the long term, perhaps farming of wild ungulates, exclusively or in combination with cattle. The project aims at modelling a dynamic interaction between humans and nature.

(<http://www.maposda.net/Global/mainglobal.htm>).

In Botswana the project is run by the University of Botswana in cooperation with the Norwegian Institute for Nature Research.

3. Objectives

The overall aim of the study is to examine and quantify variation in rodent species diversity and abundance in relation to land use and distance to pans. The aim is, partly, to learn how abundance and species diversity of small mammals vary with different land use and partly to learn how the patterns of small mammal species diversity, abundance or morphology vary with distance from pans, given different vegetation cover, grazing impact, soil structure etc. Based on the above I will discuss how this knowledge can be used in order to make land use more sustainable.

The main hypothesis is that small mammal abundance and species diversity increase with increasing grass cover, thus increasing with reduced grazing impact. This would mean that areas with less grazing impact by domestic animals would show higher small mammal abundance and diversity. It also would mean an increasing small mammal diversity and abundance with increasing distance from pans. In livestock grazed areas, small mammals are expected to respond to the piosphere pattern (deriving from Greek, "pios" meaning drink) (Perkins, 1991) meaning that the impact of large herbivores is many times higher close to the watering point, resulting in a zonation of vegetation with distance from the watering point or village (Andrew, 1988).

Trough this knowledge, combined with other studies in the MAPOSDA-project, the study aims at identifying ways to maintain biological diversity while making land-use more sustainable in the area. In short:

- **How do small mammal species richness and abundance vary with landuse?**
- **How do small mammal species richness and abundance vary with distance from pans?**
- **What are the underlying reasons for the variation?**

4. Study area

This study was done in the Kalahari savanna in southwestern Botswana with the Matsheng villages (Hukuntsi, Tshane, Lokgwabe and Lehututu) as base (approximately 24°00' S and 22°00' E)(Figure 1). The area is remote, approximately 550 km west of the capital, Gaborone.

Two climatic seasons can be clearly distinguished, a dry winter season from April to October and a rainy summer season from November to March. The area has a mean annual rainfall of ca 300 mm,

with a coefficient of variation of 50 – 60 % in the whole area (Pike, 1971). Temperatures are moderate with a summer mean (January) of ca. 26°C and a winter mean (July) of ca 11°C (Botswana Weather Bureau, unpublished). The study area is a semiarid to arid savanna landscape devoid of surface water for most of the year (Thomas & Shaw, 1991) and average elevation is 1000 – 1100 metres above sea level (Thomas & Shaw, 1991). The soils in the area are mainly desert and sub-desert soils, deep to very deep, well to excessively drained, yellowish brown to dark red, coarse sands to loamy fine sands. The Kalahari savanna vegetation ranges from areas dominated by tufted perennials and annual grasses, with sparse shrub and tree coverage in the southwest, to denser shrub-grass systems in the more humid areas further north. (Thomas et al. 2000). The study area is covered by various types of shrub savanna (Skarpe 1986).

The study area has an average population density of less than one person/km², with most of the people concentrated to the villages. The area is economically among the poorest in the country and people meet their needs through a combination of livestock, arable agriculture, wildlife, veld (field) products and Government handouts. In addition, employment elsewhere is of critical importance to the local population. (<http://www.maposda.net/Global/mainglobal.htm>)

In the 1970's the State Lands in Botswana, including the study area, were, by Botswana Government, divided into three different land use categories, according to The Tribal Grazing Land Policy (TGLP). The Communal Grazing Areas (CGA) are close to the villages and are areas meant for the villagers' livestock and other subsistence use, resulting in large grazing impact. Fenced TGLP ranches (FR) were set up to promote a commercial livestock production by the larger cattle owners. The Ranches are governmentally owned, fenced areas leased by one or a couple of families, where the owners or, most commonly their employees live on the properties. The ranches are usually put together to a large coherent cluster, as is the case in the Ncojane ranches (the ranch area studied, in the northeastern part of the study area).

Other areas were left as reserve land. Many of these areas have later been defined as Wildlife Management Areas (WMA), covering approximately 22 % of the country. The WMAs were created on initiative by the Department of Wildlife and National Parks (DWNP) as a response to the need for conservation and controlled utilisation of wildlife (Carter, 1983). Here livestock grazing is restricted and consumptive and non consumptive utilization of wildlife, including controlled hunting is carried out, both by tourists and locals (Brundin, Karlsson 1999). The WMAs function as buffer zones for the National parks and Game reserves in Botswana and are, at the same time, migratory corridors. They are also used for gathering of food, medicines, materials for handicraft etc. as well as for eco- and etnotourism. In the National Parks (NP) which cover as much as 18 % of the total land area, hunting and pastoralism is strictly prohibited and the number of people passing in and out is controlled and limited.

The aim of the present study to include many different pans with different land-use led to a relatively large study area from the Ncojane ranches in the north to the northern parts of the Kalahari Transboundary National Park in the south, a distance of roughly 200 kilometres, as the crow flies. Four of the pans studied are within the Communal Grazing Areas close to the Hukuntsi village (Hukuntsi pan, Pepane pan, Kakwe pan and Kwakai pan). Another four pans lie in the Wildlife Management Areas (Masethleng pan, Tshotswa pan, Bohelabatho pan and Ngwatle pan). One pan studied lies in the Kalahari Transfrontier National Park, KTNP, former Gemsbok National Park (Thupapedi pan) and two pans (Khiding pan and Mpaathutlwa pan) in the Mabuasehube Game

Reserve which is included in the National Park. Two pans studied lye on the Ncojane Ranch (within ranch LJ-17 and ranch LJ-23 (Mutton-chop pan)) (Figure 1)

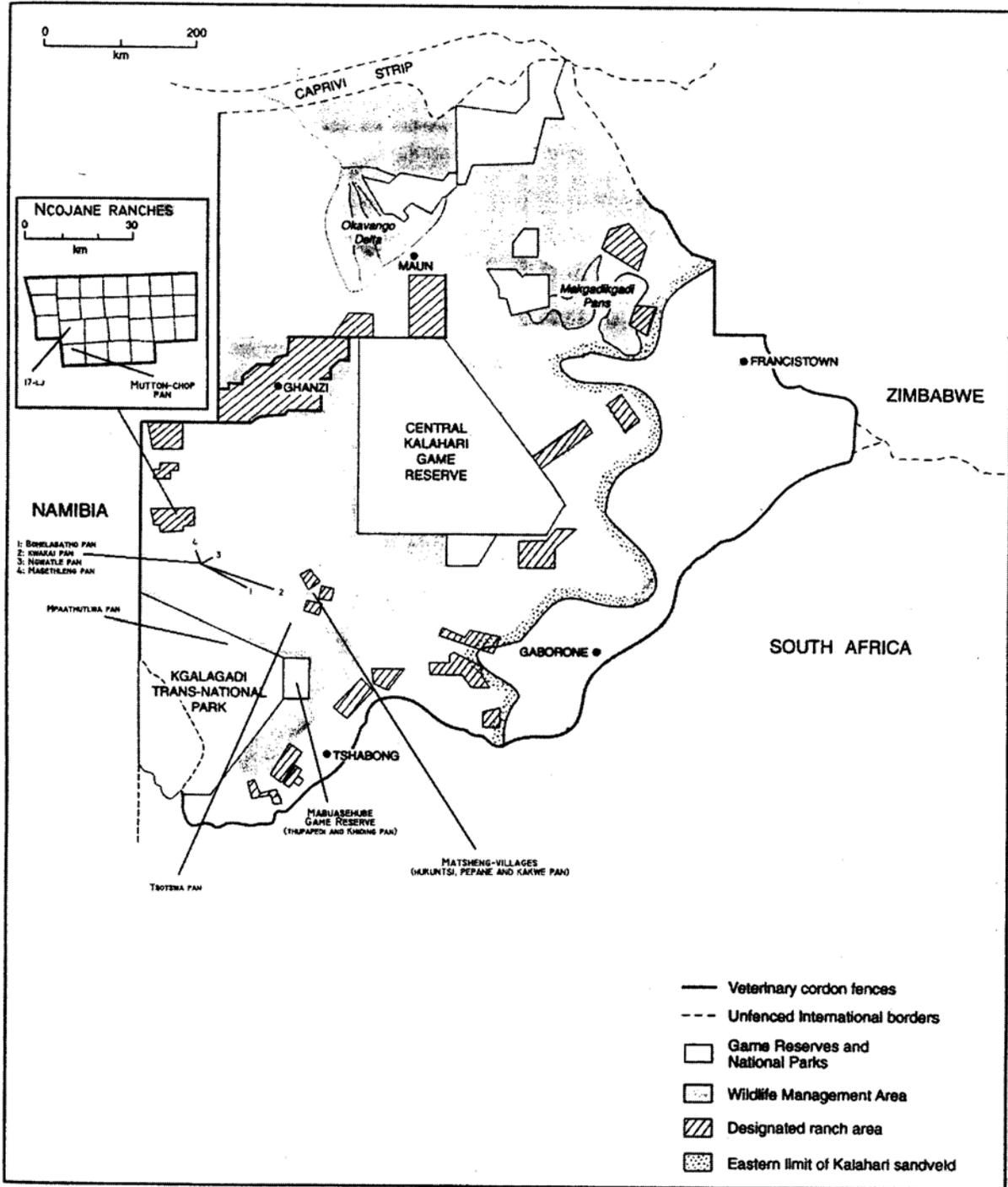


Figure 1. Map of Botswana and the study area. The studied pans are marked with arrows.

5. Methods

5.1 Field methods

The fieldwork was conducted during the dry winter season, between 15th July and 17th September 2002. Using a capture-mark-recapture method, the small mammals were surveyed in four landuse types, Fenced Ranches (FR), Communal Rangelands (CR), Wildlife Management Areas (WMA) and totally protected conservation areas, the National Park (NP), along transects from pans in the study area. Small mammals referred to are rodents and terrestrial insectivores with a body weight less than ca 2 kg.

5.1.1 Transect design and sampling sites

Pans in each of the four different management areas were chosen to represent its land use as correctly as possible (i.e. variation in number of livestock), giving a possibility for comparison between the land use types. In connection to the 13 different pans (4 in the CR, 4 in the WMA, 3 in the NP and 2 in the FR) in the study area a transect was laid out straight north-, east- or westbound reaching 5 kilometres from the pans. The aim was always to choose a northbound transect but when there were obstructions such as villages, other pans etc. east or west was chosen as transect direction. South of most pans is a large sand dune, why this direction was avoided and only one transect reaching south was chosen. Each transect consisted of 24 sampling sites, each site with two traps. Site one (picked by deciding a preset position on the GPS to make it as objective as possible) and site two were at the absolute fringe of the pan (distance 0 metres from the pan) 100 metres apart, site three and four were placed 100 metres farther from the pan fringe also 100 metres apart. In that pattern traps were placed at every hundred metres until 300 metres, whereafter traps were placed at a 500, 600, 1000, 1100, 2000, 2100, 5000, 5100 metres distance from the pan (Figure 2). The length of the transect was more than 5 km from the pan edge to ensure that the whole gradient to unaffected savanna would be included in the transect (fig. 2).

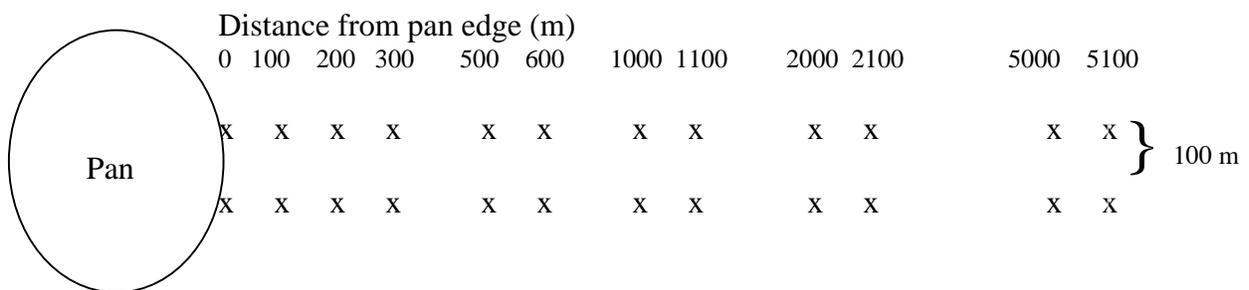


Figure 2. Sampling design in relation to a pan. x marks the positions of the sampling sites, each with two traps

A GPS-receiver was used to determine the correct placement for each sampling site within approximately 5 metres navigational accuracy. To avoid subjectivity the sampling site was fixed two metres in direction of the transect from the place where the targeted coordinates were first received. The sampling site was a 1.5 x 1.5 metre plot with the midpoint picked out by the GPS and with two sides parallel to the direction of the transect. In each plot, total canopy cover of live vegetation,

cover of dead but attached vegetation (standing litter) and detached litter cover were estimated as a percentage of the total plot area. The cover of attached grass was estimated separately and the average grass height was measured in centimetres with a folding ruler. Grass volume was calculated as cover x height. Forbs, dwarf-shrubs, shrubs and trees were divided into four height categories (0–0.5 m, 0.5–1 m, 1–2 m, >2 m) and the coverage of each height category was estimated as a percentage of the whole plot area. In addition to the sampling plot vegetation analyses, large-scale vegetation cover estimates were also done. Cover (in percentage) was estimated in four categories for each of the grass-, shrub- and tree layer: no, low, medium or high coverage. The area of estimation was a square of 100x100 m, with the corners defined by the sampling sites. The categories were defined as follows:

no = 0% (for all vegetation types)
low = 1 – 30% (grass), 1 – 20 % (bushes), 1 – 10 % (trees)
medium = 31 – 60 % (grass), 21 – 40 % (bushes), 11 – 20 % (trees)
high = >60 % (grass), >40 %, (bushes), >30 % (trees)

Trees and bushes were separated, with trees defined as having only one stem and no branches lower than 2 m from the ground. Though recording of height may be customary, this was not done as, from a small mammals point of view, this is presumably irrelevant.

5.1.2 Traps and captures

Traps were set up within 0.5 m from the centre of the plot, the GPS point. The traps were all set on day one and then checked, rebaited if necessary and reset if snapped, once a day for three consecutive days, thus, giving at best three trap nights for each trap. Due to the uneven number of trap nights in each land use area much of the data were transformed into comparable units, capture /100 trap nights.

Collapsible and ventilated Sherman's live traps were used. One medium sized and one large sized trap (measuring 76.2 x 88.9 x 228.6 mm and 76.2 x 82.6 x 304.8 mm respectively; Sejoie, 1999) were placed at each station. A mixture of peanut butter, rolled oats (oat meal) and syrup was used as bait.

The trapped rodents were:

- identified to species (following Skinner and Smithers, 1990), in the field, if possible, or after dissection
- measured (to millimetres) in body length, tail length (giving total length which equals tail + body length) and hind foot length using a metal ruler
- weighed (to grams) with a spring balance
- sexed
- classified into two reproductive categories: sexually active or not active
- marked with nail polish, giving them a number code to enable individual recognition (to avoid recording the same individual twice and to be able to estimate population sizes) (fig. 3)

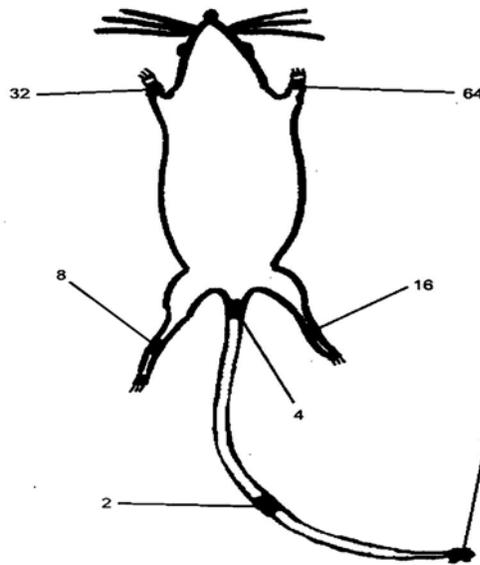


Figure 3. The method for marking the captured rodents.

If it was not possible to determine species in the field, the animal was killed by placing the animal with a cotton ball soaked in ether in a plastic bag, and dissection was carried out. Using scalpel and tweezers the skull was cleaned from skin and tissue, enabling species identification by examination of tooth and skull structure. Skinner and Smithers (1990) was used for identification.

Animals caught were marked using nail polish (Fig. 3). Individual nr 1 was marked at the end of the tail, nr 2 on the middle of the tail, nr 3 at the end and the middle of the tail (giving 2+1) etc.

Reproductive condition was evaluated externally. Females were regarded as sexually active if vagina was perforated, males if testes were descended (scrotal) (Wirminghouse and Perrin 1993; from Sejoe 1999).

Other animals than mammals were sometimes captured in the traps (i.e. lizards and birds), but such animals were released and not accounted for.

During the study period the weather was clear, with 25 – 30 °C during the day and 0 – 5 °C during night, except for two days of light showers resulting in only a few millimetres of rain.

5.2 Data analyses

The data collected in the field study were subsequently transferred to Microsoft Excel and analysed partly in Excel and partly in Minitab. In the analyses of the data mainly four spatial scales were

considered. The largest scale was the four land use categories, followed by the transects, named after the pans. On the smaller scale the sampling plots were either combined four and four to create one unit (a 100 x 100 m square with 4x2 traps), or one sampling plot represented one unit of 1.5x1.5 m with 2 traps.

Most data did not follow normal distribution even after transformation (log-transformation). Therefore the non parametric Kruskal-Wallis test and regression-analyses were used (in Mini-tab). In the Kruskal-Wallis tests differences with a p-value less than 0,05 were considered significant. In the regression analyses the r^2 - value is used, where a value between 0 and 1 is shown. The closer the value is to 1 the better the change along the x-axis explains the change on the y-axis. A r^2 -value of 0 means that no variation in the y-variable is explained by the variation in the x-variable. When analyzing the captures along the pan transects the analyses were made on the actual numbers captured (figs. 9, 10-13) while total abundance and frequency of species under different land use are shown as captures per 100 trap nights (figs. 7 and 8).

The utilization ratio of areas with different vegetation characteristics was calculated by dividing the proportion of small mammals captured on each site category, by the proportion of that site category of the total number of sites:

$$\text{Utilization ratio} = \frac{\text{number of captures at each site} / \text{total number of captures}}{\text{number of sampling plots of each category} / \text{total number of sampling plots}}$$

6. Results

6.1 Gradients

Mean volume and mean height of grasses differed between the different land use types ($p < 0.0001$). There is thus a tendency for larger volume and height of grasses in National Park and Fenced Ranches than in Wildlife Management Areas and Communal Rangelands (table 1).

Table 1. Mean grass height, cover and volume in the different land use areas. Data used from sample site vegetation estimates (100 x 100 m). Data pooled from all pans. NP = National Park, FR = Fenced Ranches, WMA = Wildlife Management Areas, CR = Communal Rangelands

Land use management	mean height (cm)	mean cover	mean grass volume (% x cm)
NP	36.1	13.6	489.2
FR	29.3	15.6	459.0
WMA	23.8	10.8	258.3
CR	17.6	6.9	122.6

There was no difference in bush/tree cover (fig. 4) between land use categories ($p=0.96$)

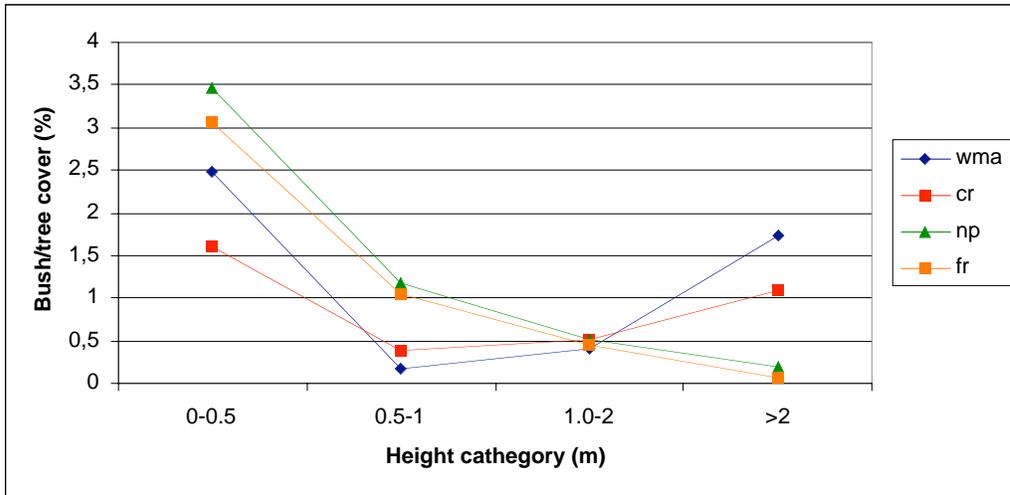


Figure 4. The mean bush/tree cover in the four landuse management areas. Data used are from sample site vegetation cover estimates.

Analyses on all the pan transects combined showed increasing grass volume with increasing distance from the pan (fig. 5). The graph shows how the grass volume on average increases with increased distance from the pan, asymptotically evening out from ~ 2000 metres.

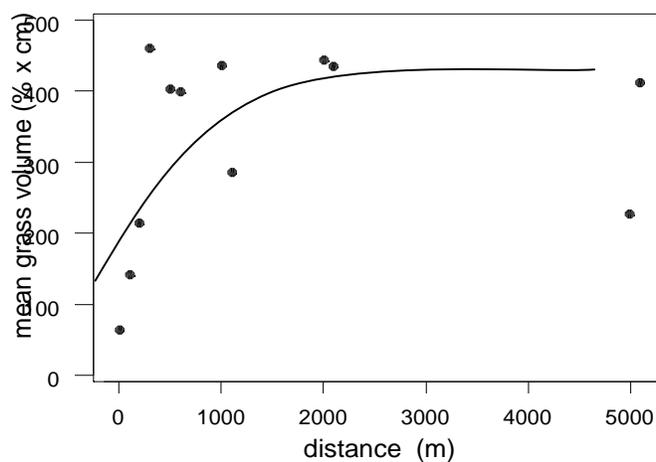


Figure 5. Grass volume (of sampling sites) varies with increased distance from the pan. Data from all the pans are pooled.

A similar compilation of the data on bush/tree cover in the sampling sites shows a reverse gradient . The graph shows how the bush/tree coverage is decreasing with increasing distance from the pan edge, also evening out from ca 2000m.

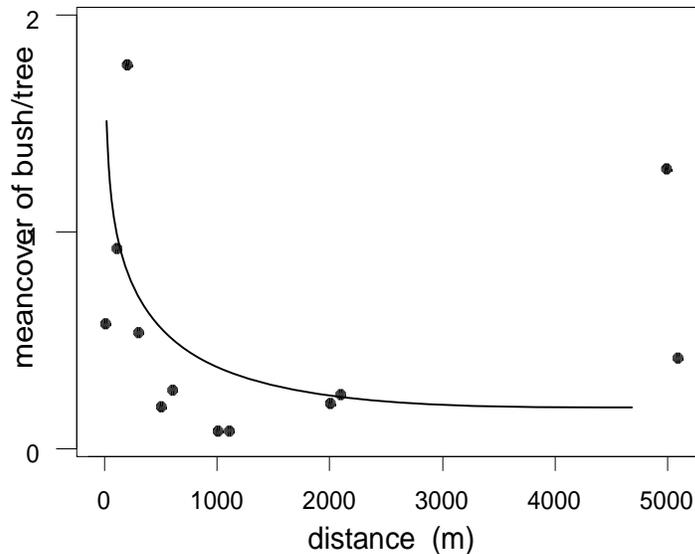


Figure 6. Mean bush/tree coverage (of sampling sites) along the pan transects, data from all pans are pooled. All height categories are included in the graph, thus no distinction has been made between bushes and trees

6.2 Trapping records

The total number of trap nights was 1872 (288 in FR, 432 in NP and 576 in WMA and CR) also counting those snapped sometimes during the night but without catch. There were 65 recaptures and 207 new individuals caught, resulting in a capture rate of 14,5 % counting the recaptures and 11 % not counting them. In total 76 females and 122 males were recorded.

In the study a total of 13 species were captured, 11 from the family Muridae, one species was from the family Gliridae and one from the family Macroscelididae (table 2). There were in total 272 captures.

Table 2. The species and the total number of individuals captured.

<u>Species</u>	<u>Number of captured animals</u>
Family Muridae (herbivores)	
<i>Acomys spinosissimus</i> – Spiny mouse (Peters, 1852)	1 ¹
<i>Aethomys namaquensis</i> – Namaqua rock mouse (A. Smith, 1834)	20
<i>Desmodillus auricularis</i> – Short-tailed gerbil (A. Smith, 1834)	1 ²
<i>Gerbillurus paeba</i> – Hairy-footed gerbil (A. Smith, 1836)	130
<i>Lemnicomys rosalia</i> – Single-striped mouse (Thomas, 1904)	1 ³
<i>Mus indutus</i> – Desert pygmy mouse (Thomas, 1910)	1 ³
<i>Tatera brantsii</i> – Highveld gerbil (A. Smith)	19
<i>Tatera leucogaster</i> – Bushveld gerbil (Peters, 1852)	16
<i>Rhabdomys pumilio</i> – Striped mouse (Sparrmann, 1784)	6
<i>Saccostomus campestri</i> – Pouched mouse (Peters, 1846)	4
<i>Zelotomys woosnami</i> – Woosnam’s desert rat (Schwann, 1906)	2
Family Macroscelididae (insectivorous)	
<i>Elephantulus intufi</i> – Bushveld elephant-shrew (A. Smith, 1836)	5
Family Gliridae (herbivores)	
<i>Graphiurus murinus</i> – Woodland dormouse (Desmarest, 1822)	1 ¹

¹ Capture in the FR

² Captured in the WMA

³ Captured in the NP

One species, *Gerbillurus paeba*, clearly dominates, constituting 63 % of the total number of individuals captured. Three species out of the thirteen constitute 80% of the captures.

6.3 Reproductive status

Out of the 41 individuals recorded as active concerning reproductive status, 32 were males and 9 females. Half way through the study it rained in large parts of the study area. Before the rain 12 out of 76 (15,8 %) individuals were recorded active, after the rain 29 out of 81 (35,8 %). No clear correlation between distance from pan or land use and the number of sexually active animals was found.

6.4 Differences in small mammal abundance and diversity under different land-use

There was a difference in the number of trapped rodents between different land-use types (Kruskall-Wallis, $p=0.002$), with the National Park having almost three times as many as the fenced ranches (fig. 7).

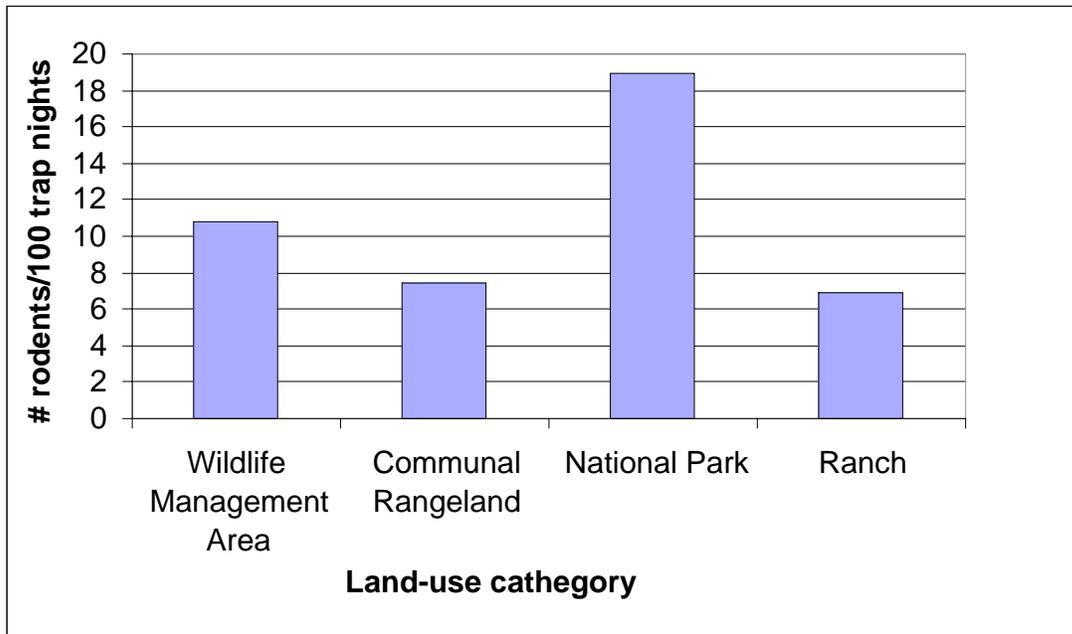


Figure 7. Abundance (number / 100 trap nights) of rodents trapped in each land-use area

Nine species were captured in the NP and the WMAs, while seven species were caught in the FRs and the CRs (fig. 8). Five species were only caught once, two of them in the fenced ranches, two in the NP and one in the WMAs.

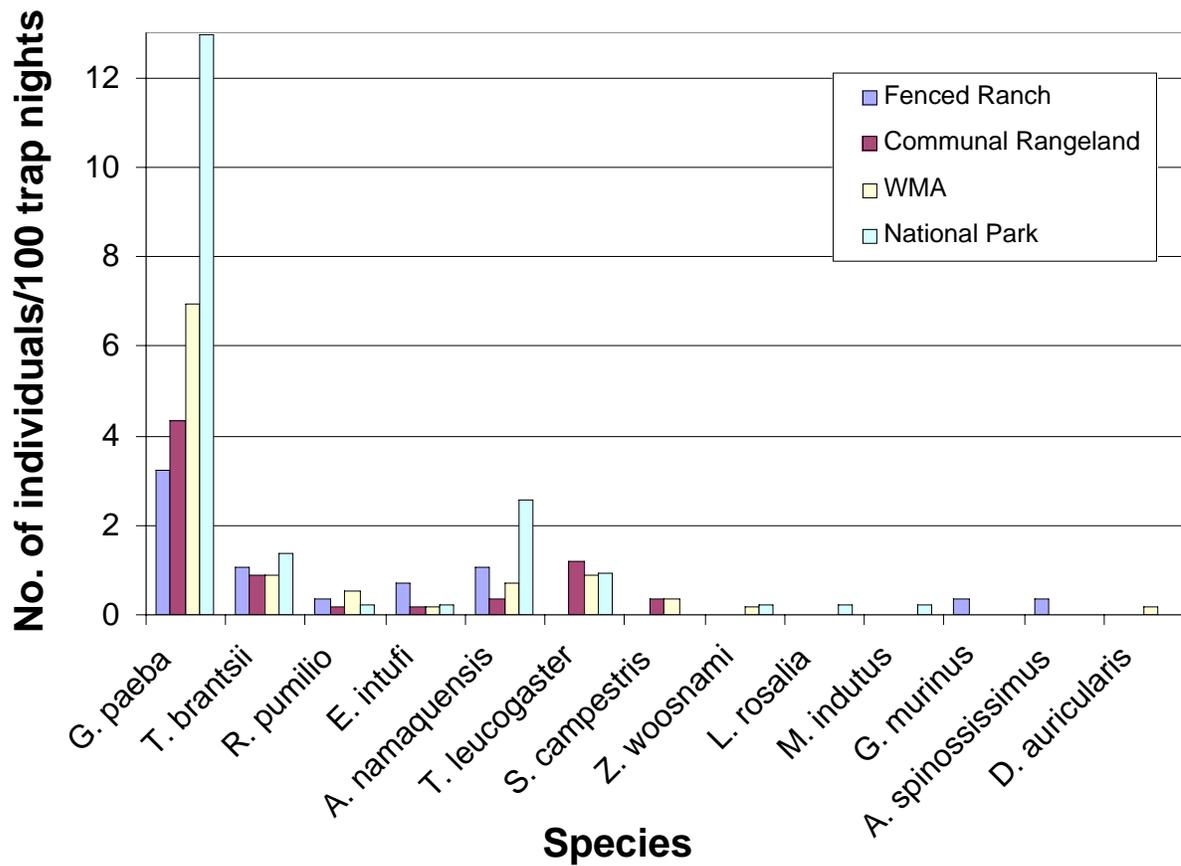


Figure 8. The number of each species that was captured in each land use area.

6.5 Differences in small mammal abundance and diversity along the transects

Along the pan transects the number of captured rodents increased as the distance from the pan increased. Figure 9 shows how many rodents, in actual numbers, that were captured at all distances, all the pans combined. The graph shows how the number of rodents, on average, increases with increasing distance from the pan until the effects of the pan subsides, at ~ 2000 metres.

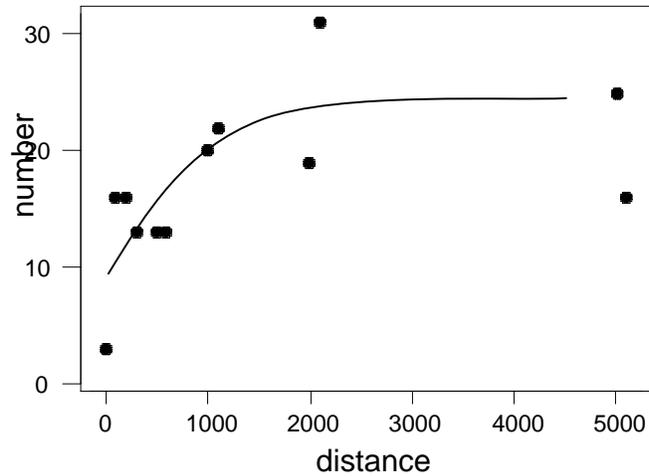


Figure 9. Number of captured individuals in relation to the distance from the pan. Data from all the pans are pooled.

The largest number of species and of species found at one distance only were caught furthest away from the pans (table 3), but there was no statistical difference in numbers of species caught with distance from pans ($\chi^2 = 1.86$, $df = 5$, $p = 0.247$).

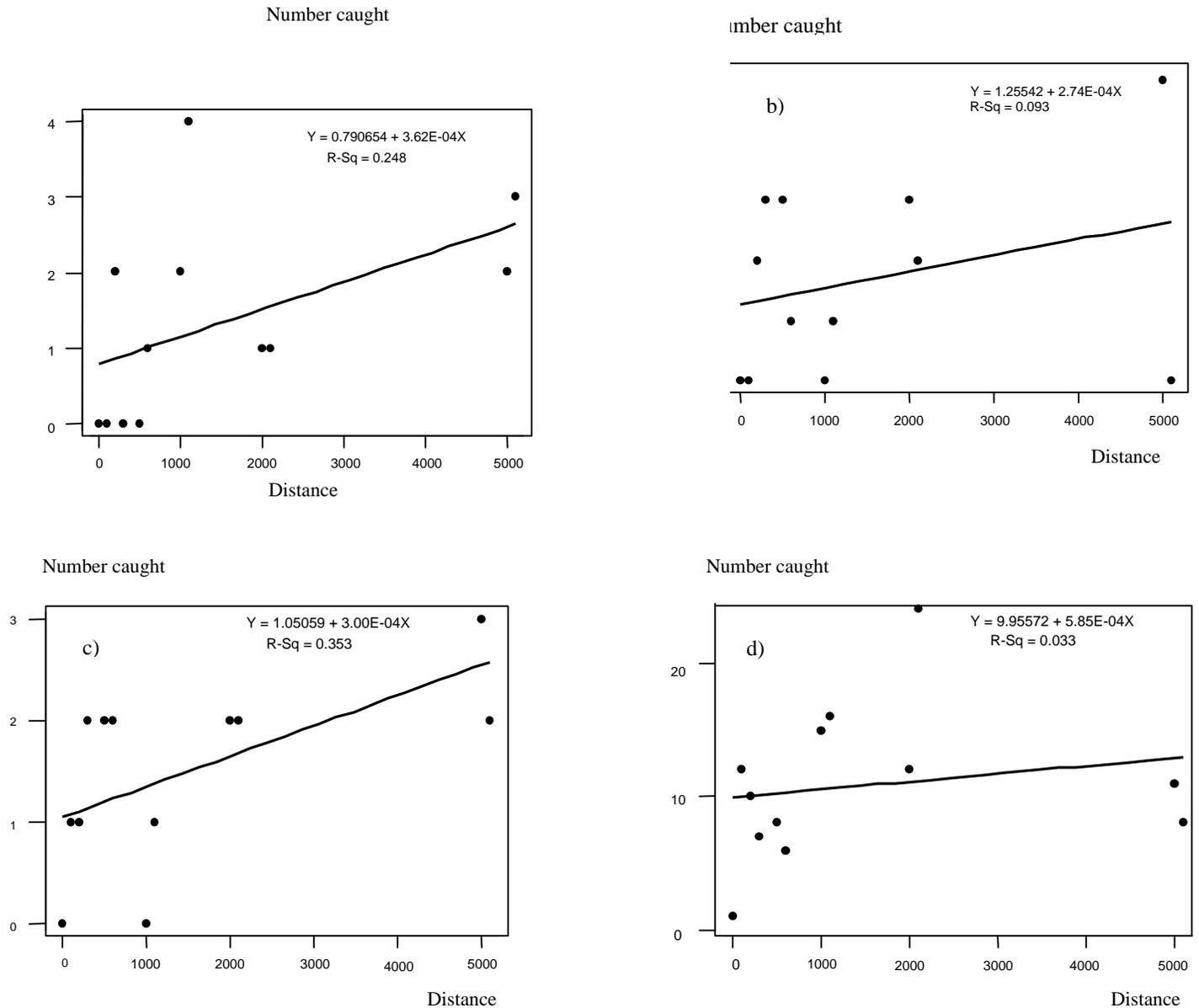
Table 3. The number of species found at different distance (100 x 100 m sites with 4x2 traps) along the transect, and the number of species not found at other distances. A total of 13 species were caught in the study.

Distance	number of species	number unique species
0-100	5	1 ¹
200-300	6	0
500-600	5	0
1000-1100	7	0
2000-2100	7	2 ²
5000-5100	8	2 ²

¹ One individual captured

² One individual captured of each species

The abundance of *A. namaquensis* and *G. paeba* showed a tendency to increase with distance from pans (fig. 10 b, d; $p=0.099$ and 0.042 respectively) There was no difference in the abundance of *T. leucogaster* and *T. brantsii* with distance (fig. 10 a, c; $p=0.335$ and 0.575 respectively).



Figures 10. Abundance of a) *T. leucogaster*, b) *A. namaquensis*, c) *T. brantsii* and d) *G. paeba* in relation to distance from the pan (real numbers with data from all the pans combined)

6.6 How small mammal abundance and diversity differ with vegetation cover

Analysis on rodent abundance in relation to vegetation cover shows that the number of rodents captured was positively related to the grass coverage in the sampling sites ($r^2 = 0.7$, $p=0.014$)

(Kruskal-Wallis). Concerning the large scale vegetation cover the actual numbers of individuals caught were: 7 individuals in areas with no grass at all (usually pans or heavily grazed areas), 55 and 56 individuals in areas with low and medium grass cover respectively, and 71 in areas with high grass cover.

Utilization ratio (U.R.) for the total number of small mammals captured, for *G. Paeba* and for all species excluding *G. Paeba*, is shown in figures 11, 12 and 13. A U.R. of 1 shows a random usage while a U.R. above 1 indicates a preference to the category A U.R. below 1 indicates an avoidance of a category. In fig. 11 all three curves have a similar pattern being highest U.R. for vegetation category with the highest grass cover. The U.R. for bushes and trees is highest at category *medium* except for analysis on all species but *G. paeba* where category *high* seems to be preferred. (Figures 12 and 13)

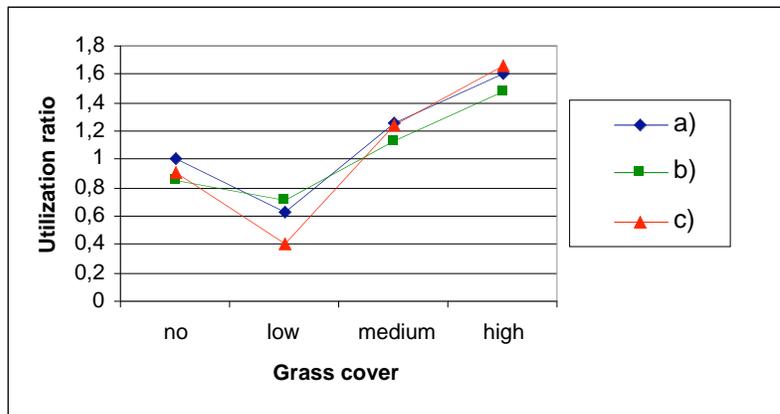


Figure 11. The U.R. in relation to large scale grass cover for a) all species combined, b) *G. paeba* and for c) all species but *G. paeba*. (cover categories based on large scale vegetation cover analysis)

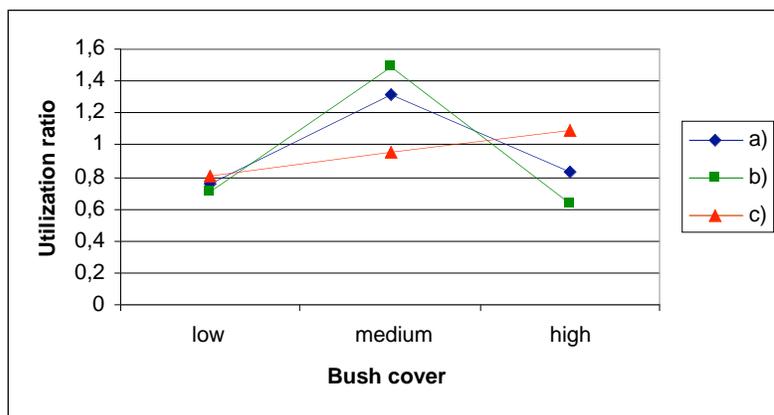


Figure 12. The U.R. in relation to large scale bush cover for a) all species combined, b) *G. paeba* and for c) all species but *G. paeba*. (cover categories based on large scale vegetation cover analysis)

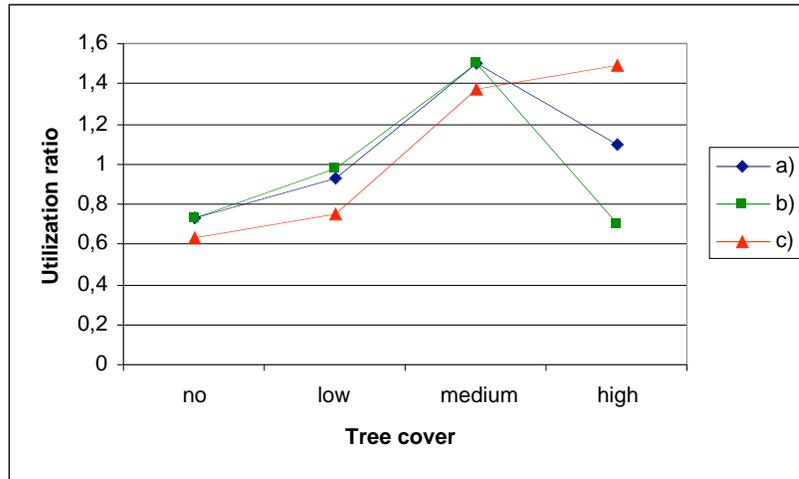


Figure 13. The U.R in relation to large scale tree cover for a) all species combined, b) *G. paeba* and for c) all species but *G. paeba*. (cover categories based on large scale vegetation cover analysis)

The actual numbers of captures were for the bush cover: no = 0, low = 49, medium = 102, high = 38; and for the tree cover: no = 36, low = 75, medium = 57, high = 21.

6.7 Recapture results

The recapture rate / 100 trap nights in the compared land-use areas was:

Fenced Ranches: 1,7

Communal Rangelands: 2,6

Wildlife Management Areas: 3,1

National Park: 4,4

Statistical test (Kruskal-Wallis) on the recapture rate showed no significant differences between land use types. The percentage of recaptured individuals per total number of captured individuals did not vary either.

Fenced Ranches: 25 %.

Communal Rangelands: 29%

Wildlife Management Areas: 28 %

National Park: 22 %

6.8 Morphology

Variation in morphological traits within species in different land use types and distances from pans were analysed for the most abundant species, *G. paeba*, *T brantsii*, *T. leucogaster*, *A. namaquensis*. The test showed a p-value of 0.065 for variation in weight of *G. paeba*, that tended to increase in

weight with increasing distance from pans. There was no variation in weight related to land use ($p=0.237$). Analysis of the other species showed similar results (*T. brantsii*: $p=0.684$, *T. leucogaster*: $p=0.239$, *A. namaquensis*: $p=0.519$). Across species, average weight varied from 16 g for *G. murinus* to 69g for *T. brantsii* (table 4).

Table 4. Compilation of all morphological data with the most abundant species first. For five of the species there was only one capture. One of these escaped (*M. indutus*) hence no data.

	Mean weight (g)	StDev weight (g)	Mean body length (cm)	StDev body length (cm)	Mean hindfoot length (cm)	StDev hindfoot length (cm)	Mean tail length (cm)	StDev tail length (cm)
<i>G. paeba</i> (n=130)	25.3	4.0	9.21	0.74	2.60	0.13	10.35	1.62
<i>A. namaquensis</i> (n=20)	39.5	7.32	10.65	1.00	2.48	0.12	13.78	1.23
<i>T. brantsii</i> (n=19)	68.5	10.45	12.78	1.56	3.49	0.24	14.37	1.63
<i>T. leucogaster</i> (n=16)	67.0	8.86	12.65	1.19	3.47	0.22	14.34	1.26
<i>R. pumilio</i> (n=6)	29.3	2.5	9.0	0.81	2.3	0.2	10.47	0.5
<i>E. intufi</i> (n=5)	45.6	10.6	11.0	1.57	3.48	0.16	11.6	0.73
<i>S. campestris</i> (n=4)	48.8	11.3	12.05	1.18	1.9	0.18	3.9	0.14
<i>Z. woosnami</i> (n=2)	53.0	9.9	10.15	1.06	2.65	0.07	10.85	0.92
<i>A. spinosissimus</i> (n=1)	22	-	8.5	-	2.3	-	7.9	-
<i>D. auricularis</i> (n=1)	35	-	6.2	-	2.6	-	5.3	-
<i>L. rosalia</i> (n=1)	32	-	9.5	-	2.5	-	10.2	-
<i>M. indutus</i> (n=1)	-	-	-	-	-	-	-	-
<i>G. murinus</i> (n=1)	16	-	9.0	-	1.7	-	8.5	-

7. Discussion

7.1 Gradients

A gradient in land use intensity or in resource availability can include a multitude of causes and effects. The livestock grazing gradient, as this study is dealing with, could manifest itself, on the larger scale, as a difference in overall grass coverage, bush coverage, trampling, dung accumulation etc. between the different land use types. Among the land use types the NP has the highest grass volume which is probably due to the absence of livestock. Consequently, the “energy limitation hypothesis” (introduced here by Aava-Olsen, 2001) seems relevant as the highest number of individuals was captured in this area. On the other hand, the high vegetation cover (and thus assumably plant productivity (energy)) in the FRs would imply an equally high number in these areas. That this is not the case could be dependent on reasons not taken to account in this study.

On the smaller scale, along the pan transects the high quality forage close to the pans (Skarpe, 1986) leads to high concentration of cattle or wild herbivores there. The grazing may be the cause of the gradient in plant biomass along the transect. The number of rodents captured seems to follow the pattern of the grass volume along the transect (figs. 5 and 9). The bush cover decreases with distance from pan. The area around the pan is probably still heavily grazed by wild herbivores but not as extensively and not with as high concentration of animals. The fact that the ranches also show a high grass volume may be a result of actions taken by the owners of the ranches, such as cutting down shrubs and evenly distributing the livestock.

7.2 Trapping records

The number of species of small mammals is high in this study compared to other studies in similar areas. Happold and Happold (1990) collected 8 species in a savanna in Malawi, Sejoie (1999) caught 6 species in northern Botswana and Rudinow Sætnan (2000) found 12 species in a small reserve in eastern Botswana. The high number of species is probably a result of a large study area and the aim of studying areas with different land use and different influence from pans. On the other hand many species were captured only once which makes it difficult to say anything about their abundance, more than the existence of this individual. All species except *Acomys spinosissimus* are previously recorded from the study area (Skinner & Smithers 1990). *A. spinosissimus*, however, is said (Skinner & Smithers 1990) to be widely distributed in Zimbabwe but only to occur in eastern Botswana. It usually occurs in rocky areas but also on sandy alluvium along rivers. This specimen was taken 2100 metres from a FR pan, but in an area still influenced by the pan with rocky pan soil and low vegetation.

Compared with other studies in subtropical Africa (Sejoie 1999, Rudinow Seatnan 2000, Happold & Happold 1989) this study turned out similar in respect of trapping results, with one species constituting a large portion of the trapped individuals. The male dominance may be explained by greater activity and mobility of males, particularly after they become sexually active.

The capture rate of 11% is also high compared to other studies on rodents in Botswana. Sejoie (1999), studying small mammals in Chobe National Park, found as low rates as 2.1 and 0.6 % on the

large and the medium traps respectively. Studies done in the Kalahari Transfrontier National Parks only (Nel & Rautenbach, 1975) had a total capture rate of 9 % in the course of four years, including both rainy- and dry- season. The use of only big and medium traps enabled catching the largest amount of rodents as the small traps exclude the larger rodents, while the large traps can catch all sizes (Sejoe, 1999). The large traps captured 125 of the 207 individuals and the medium traps captured the rest, 82 individuals, confirming what other studies have shown: a tendency of greater number of captures in the bigger traps (Sejoe 1999, Nel & Rautenbach, 1975).

A small percentage of the trapped individuals got away during handling; all of those individuals were identified to species and weighed, though not properly measured why a few values are missing.

It is interesting to note that the study on insects conducted at exactly the same location and time by Åström (2003) came to conclusions quite opposite to those shown in this paper. The insects, as opposed to the small mammals are, in short, instead favoured by the presence of livestock .

7.3 Sexual activity

The rain during the study came ahead of the rainy season and was only a light drizzle, still it seems there was a quick response in the rodents' reproductive status. The percentage "active" more than doubled after the rain. Most likely, the rain triggered the increase in reproductive activity. It is unlikely that the rain coincided with the time of the year when the number of "active" in the sense of reproductive state are increasing, as the rainy season, usually triggering the start of the reproductive period (Sejoe 1999) was still two months ahead.

A correlation between land use, distance from pans and the number of sexually active individuals could not be calculated as e.g. all the animals captured in the National Park were capture after the rain. Data showing a higher frequency of active individuals in this area could both indicate a higher reproductive state overall and that the rain had an effect on the reproductive status.

7.4 Differences in small mammal abundance and diversity under different land use

The species diversity and the number of individuals of small mammals, were slightly higher in the National Park and the WMAs than in the CRs and the ranches. Other studies have shown a larger number of species being captured in areas from which cattle have been excluded (Keesing, 1998), and where wild herbivores have been excluded (Rudinow Saetnan, 2000). In my study there was a gradual reduction in livestock grazing, from the National Park with no cattle grazing (total enclosure) to the FRs and the CRs with large grazing impact (as mentioned earlier the pans with no livestock are, of course, also grazed, but not as intensely). Perhaps the difference in grazing also explains why two species more were captured in the National Park and the WMA compared with the other two land-use types. Although there is relatively small difference between grass volume in the NP and FR the difference in the number of individuals is significant ($p=0.002$). There may be several different explanations for this such as different kinds of grass (palatable or non-palatable) or different kinds of disturbance (from wildlife or human and cattle). It is interesting to note that Nel & Rautenbach (1975) showed that it is not the relative carrying capacity of a habitat that reflects the number of species, but the available number of niches. Consequently, this may explain the fairly small difference in the number of species this study shows between the land use areas, as a transect

may hold an equal amount of niches heavily grazed or not. The reduction in grass cover and its substitution with shrubs in some parts of the gradient/transect may create, even though in a more harsh environment, a new niche and possibilities for another, more persistent species to prevail (Nel & Rautenbach, 1975).

7.5 Differences in small mammal abundance and diversity with distance to pan

The distance to pans seems to be important for the abundance of small mammals, increasing with the distance to pans, probably owing to the increase in grass cover and grass height with increasing distance. The driving force may, as in the difference between landuse regimes, be variation in large herbivore activity. The correlation seems to be linear up to about 23 catches per 100 trap nights after the influence of the pan ceases at about 2000 m distance (fig. 9). This is the same distance where the pan effect on the grass volume ceases (fig. 5). Also species composition varies along the gradient, and 4 of the five species captured only once were encountered beyond 2 km, the fifth was taken at the pan's edge.

The number of individuals increases along the transect (until ~2000 metres) as well as the number of “new” species not found anywhere else along the transect. Only two species (*G. paeba* and *A. namaquensis*) showed significant or close to significant increase along the transect. The increase in number of individuals indicated in figure 9 is probably a result of the capture rate of these two species since they are the two most abundant species in the study, constituting nearly three quarters of the total number of captures. Had this been a more extensive study, with more captures of the species with low capture rate, maybe these species also would show a similar pattern.

One could argue that, since the pans have high quality, mineral rich vegetation, the small mammals would decrease with distance from the pan, rather than increase. This could especially be the case in the more remote areas where the pans are less affected by livestock grazing. In these areas the high quality forage closer to the pans (Skarpe, 1986) would point to a higher “energy level” inherent in the habitat and thus, according to Aava-Olsson (2001), sustain a higher number of individuals. It seems, however, that there are other factors, including, e. g., impact by wild large herbivores on vegetation cover, suitability of the substrate for burrowing and abundance of small and medium sized predators, leading to a increase in small mammal abundance with distance to pans. Looking at the transect as a whole the pans probably contribute with a higher heterogeneity in the landscape and imply those “rare resources” (Aava-Olsen) mentioned earlier, assumably creating new niches and sustaining habitat for a larger number of species.

7.6 How rodent abundance differs with vegetation coverage

Trampling and grazing have been shown, for instance in north American rangelands, to reduce the lower vegetation cover for small animals (Grant et al., 1982), thus increasing their exposure to predators (Birney et al., 1976; Edge et al., 1995) Other influences may also occur such as trampling affecting the burrowing substrate for the rodents.

Figure 11 shows a preference of small mammals to areas with high grass cover. To rule out the possibilities of patterns being affected by the big number of species (two different species can have totally different habitat preference and different dependence on a certain grass cover), the most

abundant species, *G. paeba*, is also shown in the U.R. analyses (fig. 11-13). Since almost two thirds of the captured individuals were *G. paeba*, all the species but *G. paeba* are also accounted for. Preference for fairly densely vegetated habitats also partly explains the high number of individuals in the National Park (fig. 7) where the grass cover overall was the greatest. The number of small mammals and the number of small mammal species have been shown to be related to the grass cover: increased grass cover increases the number of individuals and the number of species (Rudinow Saetnan, 2000; Keesing, 1998). The low number of small mammals captured in the FR, although the grass “volume” compared to NP is similar, indicates that other factors also influence the abundance, e.g. species of grass, the quality of the soil, trampling, availability of water, and other factors not surveyed in this study. The lower number of trap nights could also affect the credibility of the results.

The number of rodents increases with the increase of bush and tree cover up to a certain point which could be the point where bush encroachment takes place keeping grass cover low and thus limiting food supplies and essential shelter for the small animals. Before that point the increase in bush cover may give better protection from avian predation for the rodents whilst the decrease in grass cover may not occur or affect the numbers. In the ranches there seemed to be an additional disturbance as the people living on the ranch cut down large amounts of bushes and trees to repress the effects of bush encroachment and give way to grass. This could possibly affect the food supply and favour species dependent on food from grass and lessen the food supply for species dependent on live bushes. In this study the bush and tree cover was recorded the same whether cut down, dead or alive, since the cover in terms of shelter from predation is assumably the same. So the effect of the disturbance for small mammals mentioned above is therefore not looked into in this paper. The utilization ratio on the other hand also shows a preference for the sites recorded as medium cover of bushes and trees with a U.R. as high as 1.5 on sites with medium coverage, dropping down to below one when bush and tree coverage was high. This also supports the argument above, that bush encroachment, keeping grass cover low, is negative for the rodents and furthermore that a certain bush cover is necessary for many rodents to avoid predation. Grass, thus, seems to serve a purpose either as food supply or possibly also as predation protection. Most small mammals captured have an omnivorous diet but seed and foliage consumption is high especially during winter (Skinner and Smithers, 1990) indicating that grass is an important factor for the small mammals’ food supply.

7.7 Recapture

The data on recaptures also showed no statistical significance. Hypothetically the recapture percentage would be the lowest in the areas with the highest abundance as a large population size would lead to a smaller risk of being captured again. Had the sample size been larger this might have supported the findings of the highest abundance in the NP. The number of recaptures was assumed not to be sufficient for estimating population sizes as some of the pans resulted in only two recaptures (on ranch LJ-17) and the pan with the most recaptures recorded (Khiding pan) were 10 individuals recaptured. The percentage of recaptures per individual was roughly the same regardless of land-use type or distance to pan probably owing to the limited mobility of the rodents (only three of the 65 individuals recaptured were recaptured in the adjacent traps, 100 metres from the trap where the rodent was originally captured). The NP shows a slightly lower recapture rate, and a lower number of recaptures together with a high number of total captures indicate a larger population than in the other land-use types.

7.8 Morphology

Morphology was mostly analysed within the four most abundant species and no differences were found between the compared land use types within the study area, maybe owing to the fact that it is not usually the fitness of the individuals that differs in stressed environments or during seasonal changes (Nel & Rautenbach, 1975). The tendency for *G. paeba* to increase in weight with increasing grass cover may suggest a larger food supply with increased grass cover, or improved protection for predation, resulting in a higher proportion in the population of old and heavy animals. On the other hand, small mammals often adopt to variation in food availability by changes in population size rather than physical adjustments (Nel & Rautenbach 1975). The declining resources are instead shared by a lower number of competing individuals. The data, however, are also easy to misinterpret as narrowing down sample criteria to only one species renders only few individuals examined. This is specially the case in the fenced ranches where only 9 individuals *G. paeba* were caught during the three trap nights at each pan. Table 4 shows a great variance in standard deviation in individual weight, in some cases more than 20 % of mean weight (*E. intufi* and *S. campestris*). This may be a result of differences in age (which was not recorded in this study) but could also include a response to habitat quality.

8. Conclusion

How do small mammal species richness and abundance vary with landuse?

There seems to be a variation in both number of individuals (significant) and number of species (non-significant) between the different land use areas. The presence of livestock appears to affect negatively on both small mammal species richness and abundance as the areas with most livestock show the smallest number of species and individuals. The land use gradient on the other hand does not show as clear connections, as the land use areas with most cattle, the FRs, do not show the least grass volume.

How do small mammal species richness and abundance vary with distance from pans?

Along the pans, the grass cover and grass volume seems to play an important role, whether as food or shelter from predation. There appears to be a grazing gradient stretching from the pan with the least grass cover closest to the pan resulting in a high bush cover. The number of small mammal individuals seems to differ accordingly (significant or close to significant concerning some species, non-significant concerning others), as well as the number of species (non-significant).

What are the underlying reasons for the variation?

It seems, thus, that the number of individuals and the number of species of small mammals is positively correlated with grass cover especially on the small scale. As discussed, the plant productivity/energy possibly creates advantageous habitat rendering larger number of individuals and species. Being a complex matter, a multitude of different factors other than this probably also play an important part, e.g. burrowing substrate, livestock trampling, forage quality etc.

In the study area dealt with in this study the Wildlife Management Areas cover a large part. The creation of these in the 1970's seems to be a good initiative, on the small mammals part, taken by the Botswana Government. With an abundance and a species diversity, according to this study, almost as good as the untouched parts of the National Park, the WMAs create better habitats for small mammals, compared to the two other land use areas studied. Concerning pans, the grazing gradient also seems to be affecting the small mammals with a decreased diversity and abundance closer to the pan.

Hence, impact on habitat quality, such as extensive livestock grazing has an impact on the smaller mammals as well as the larger wildlife as shown both in this study and others. Increasing grazing leading to a widely spread bush encroachment combined with a deteriorating grass cover results in a decline in the number of small mammal species and abundance.

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