

Influence of variations in land use intensity on species diversity and abundance of small mammals in the Nama Karoo, Namibia

Anke Hoffmann and Ulrich Zeller

Museum für Naturkunde, Institut für Systematische Zoologie, Invalidenstr. 43, 10115 Berlin, Germany

Corresponding author : Anke Hoffmann, e-mail : anke-hoffmann@gmx.net

ABSTRACT. The influence of the intensity of land use on small mammals in the ecoregion Nama Karoo, Namibia was investigated within the biodiversity programme BIOTA. Changes in species diversity and abundance were investigated across a fence separating heavily grazed communal and lightly grazed government owned rangeland. Assessing and monitoring of the small mammal populations were done seasonally from 2001-2003 on each of 2ha plots by using capture-mark-recapture methods. In total, 311 individuals representing nine species were caught within 5760 trap nights. Species richness, total abundance, species diversity and settlement was lower in the overgrazed area. The most abundant species were the Gerbillinae, *Gerbillurus vullinus* and *Tatera leucogaster*. *T. leucogaster* did not occur in the overgrazed area. Due to the loss of grass cover, smaller bush diversity, bush encroachment and smaller arthropod abundance in the overgrazed area, changes in the small mammal community were most likely caused by the loss of food resources, available dew, disruption of habitat structures, cover and shelter and by increased predation risk. Only the 'desert' species, *G. vullinus*, was favoured by the degraded land. It is also obvious that the uncontrolled grazing in the communal lands has affected the biodiversity and the regeneration potential, thus leading to land degradation.

KEY WORDS : Namibia, Nama Karoo, fence-line contrast, land use, rodent ecology, *Gerbillurus*, *Tatera*.

INTRODUCTION

Small mammals are important components of arid and semi-arid ecoregions : as consumers (KERLEY, 1992a), predators and dispersers of seeds (PRICE & JENKINS, 1986), burrowers and as prey for carnivores and raptors (KOTLER, 1984; HUGHES et al., 1994). Changes of habitat structure and complexity are associated with changes in small mammal community structure and species richness (DELANY, 1964; ROSENZWEIG & WINAKUR, 1969; BOND et al., 1980; GRANT et al., 1982; ROWE-ROWE & MEESTER, 1982; KOTLER, 1984; ABRAMSKY, 1988; KERLEY, 1992b; ELS & KERLEY, 1996; HOFFMANN, 1999; AVENANT, 2000).

Large herbivores can modify the vegetation layer in terms of structure and species composition to a level where small mammals are affected (BOWLAND & PERRIN, 1989; KEESING, 1998; HOFFMANN, 1999). An ecological disturbance of the habitat is often associated with decreases in small mammal diversity. Therefore biodiversity of small mammals can be used as an indicator of disturbance in an ecosystem.

Most of the Karoo ecoregion in Namibia is rangeland for livestock grazing (HOFFMAN et al., 1999) and heavy grazing has left parts seriously degraded (LLOYD, 1999). Livestock grazing has been identified as the major threat to biodiversity in that region, but also mining, agriculture and alien invasive plants are significant threats (LOVE-GROVE, 1993; LLOYD, 1999). In general most investigations on the effects of grazing in rangelands have centred

on vegetation (NOY-MEIR et al., 1989; OLSVIG-WHITTAKER et al., 1993; TODD & HOFFMAN, 1999); with only a few studies on how the extent of grazing influences arthropod assemblages (DEAN & MILTON, 1995; RIVERS-MOORE & SAMWAYS, 1996; SEYMOUR & DEAN, 1999; HOFFMANN et al., 2003). Investigations on the effect of different land use practises on small mammal assemblages in Africa are scanty (KERLEY, 1992b; NYAKO-LARTEY & BAXTER, 1995; MONADJEM, 1999).

The aim of this study was to determine the influence of different land use intensities on the diversity of small mammals. Within the interdisciplinary biodiversity programme BIOTA (Biodiversity Monitoring Transect Analysis in Africa; cf. ZELLER, 2003) a study on the population ecology of small mammals has been carried out in the Nama Karoo, southern Namibia. This study was carried out in the heavily grazed communal rangeland and a neighbouring moderately grazed rangeland, used for Karakul breeding purposes, to address the following questions :

- (1) Does small mammal species richness, abundance and diversity differ between overgrazed and moderately grazed areas?
- (2) Does heavy grazing influence the composition of small mammal assemblages?
- (3) Which species, if any, are most affected by the habitat changes? Does it favour any species?

MATERIAL AND METHODS

Study area

The Nama Karoo occurs on the central plateau of the Cape Province in South Africa, and extends over the Orange River into Namibia in the northwest, where the study was conducted. This ecoregion is described as a vast, open, arid region dominated by grassy dwarf shrubland with summer rain and climatic extremes, where droughts are common (VENTER et al., 1986; DEAN & MILTON, 1999). Most of this ecoregion is rangeland for livestock grazing (HOFFMAN et al., 1999); less than one percent of the Nama Karoo is protected (COWLING, 1986; BARNARD et al., 1998). The region is characterized by fence-line-contrasts caused by varying land use practises.

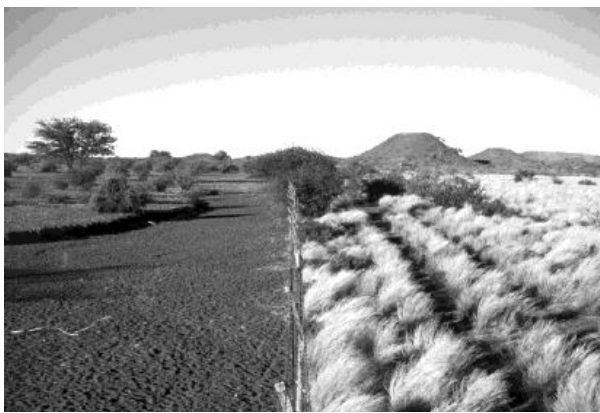


Fig. 1. – Fence-line-contrast of the study sites. Left : overgrazed communal farming area of Nabaos; right : moderately grazed governmental farming area of Gellap-Ost.

The study was conducted on two neighbouring areas with different land use practises (Fig. 1), approximately 20km northwest of Keetmanshoop. One study plot was highly overgrazed, mainly by goats within Nabaos communal area (26°23'26"S, 17°59'43"E). The other plot (distance 1.5km) was within the government Karakul sheep breeding farm in Gellap-Ost (26°24'04"S, 18°00'17"E). In contrast to the uncontrolled grazing in Nabaos, Gellap-Ost uses a rotating grazing system with a lower stocking rate. Free-ranging ungulates like Kudu (*Tragelaphus strepsiceros*) and Steenbok (*Raphicerus campestris*) were rarely observed.

There are three main seasons : hot/wet (January-April) cold/dry (May-August) and hot/dry (September-December). Rainfall occurs in summer from January to April and averages 150mm per year (cf. MENDELSON et al., 2002). In 2002 rainfall averaged 178mm, but in 2003 there was drought, with only 55mm of rainfall. The mean monthly temperature range was 2002 22°-37°C (maximum) and 8°-20°C (minimum).

Trapping

Trapping was conducted on two 2ha grids which were separated by a fence and 1.5km apart. Each grid consisted of 90 Sherman standard live traps spaced by 15m intervals. Capture-mark-recapture methods (CMR) were used during trapping sessions of 4 consecutive trapping nights

in each plot. The investigations took place at different seasons per year. Traps were baited with a mixture of peanut butter, oats, mashed bananas and bird seeds. These were set before sun set, checked at night and in the morning. In the second study year, day trapping was done in addition. Captured animals were weighed, sexed and body measurements and reproductive status were recorded. Each animal was individually marked by using a subcutaneous tattoo on the underside of the tail's base (HUGO, 1990; cf. HOFFMANN, 1999).

Data analysis

The term 'trap night' is used to describe one trap which was set for a 24h period (ROWE-ROWE & MEESTER, 1982). Trap success was calculated as the number of captured individuals/100 trap nights. Abundance was used because it differed only by 1.2% from the Minimum Number Alive (MNA) (cf. BRONNER & MEESTER, 1987). For species diversity calculations the Shannon Wiener diversity index (Hs) was chosen. For survival calculations, new individuals of the last trapping session were not considered. Those which were trapped only in one trapping session, 'survived' at least for one week.

Assessing and monitoring environmental features

For understanding the interrelation between small mammal coenosis and their habitat different environmental features were assessed and monitored. Data on rainfall and temperature were given by a BIOTA computer controlled weather station near the Gellap-Ost observatory. Bushes were counted, their sizes estimated in four categories between \varnothing 0.5 - \geq 2.0m and mapped. Ground vegetation cover per plot was estimated within ten 4m²-frames by using the Londo-scale (LONDO, 1975) and then extrapolated. Also plant phenology was monitored over the study period. Arthropod sampling was done using 10 pit-falls per plot over 8 days, to assess and monitor changes of epigeic arthropod abundance (cf. VOHLAND et al., 2005). Small mammal burrows were counted and mapped once in both plots in October 2002. Observations of potential small mammal predators were recorded.

RESULTS

Habitat features of the study plots

In Nabaos, no grass layer existed all year round. In Gellap-Ost the dominant grass species *Stipagrostis uniplumis* (height app. 50cm) covered the ground by up to 10%. Herbs occurred mainly after the rain. Bush cover was generally low (Nabaos : 2.5%, 488m², 1382 ind.; Gellap-Ost : 2.1%, 415m², 685ind.). More large bushes ($\varnothing \geq$ 1.5m) were found in Gellap-Ost, where bushes covered an area 1.6 times larger than that in Nabaos. *Rhigozum trichotomum* was the dominant bush in both plots, whereas *Catophractes alexandri* and *Calicorema capitata* were the subdominant species in Gellap-Ost, and Nabaos respectively. Both *Boscia foetida* and *Phaeoptilum spinosum* were also abundant in both plots. Bush diversity was lower in Nabaos (Hs 0.96) than in Gellap-Ost (Hs 1.28).

All burrows were located in bushes in Nabaos, whereas only 61% were in bushes in Gellap-Ost. The rest of the

burrows were in the open grassland. Twelve percent (out of 25) and 37% (out of 90) of the burrows were occupied by small mammals in Nabaos and Gellap-Ost respectively.

In total, within 1280 trap nights 16713 epigaeic arthropods in 19 orders (without mites and collembola) were collected and were composed mainly of ants, with 9466 specimens, beetles with 1673 specimens, and termites, with 747 specimens. Most animals were trapped in May in both years, after the rainy season. In Nabaos the arthropod activity was lower and only 38% of the ground active arthropods were trapped.

Potential predators of small mammals in the area were the Spotted Eagle Owl (*Bubo africanus*), Pale Chanting Goshawk (*Melierax canorus*), Black-backed Jackal

(*Canis mesomelas*), Bat-eared Fox (*Otocyon megalotis*), Cape Fox (*Vulpes chama*), Caracal (*Felis caracal*), mongooses and various species of snakes.

Species richness

Between October 2001 and August 2003, eight trapping sessions per plot were conducted. Out of a total of 5760 trap nights, 311 individuals (911 captures) representing nine species were caught and marked (Table 1). The mean species richness in Nabaos was 3.3 (range : 2-6) and in Gellap-Ost 5.4 (range : 4-6) (Fig. 2). The mean monthly trapping success was 4.79 ± 2.33 for Nabaos and 10.42 ± 6.32 for Gellap-Ost. The overall trap success in Nabaos out of 2880 trap nights was 3.75 and 7.05 in Gellap-Ost.

TABLE 1
Species richness
Listed are all captured species and the total of recorded individuals within 5.760 trap nights.

per plot 2880 trap nights	Nabaos		Gellap-Ost	
	ind.(n)	%	ind.(n)	%
Macroscelididae				
<i>Elephantulus intufi</i> (A. Smith, 1836)	1	0.92	9	4.46
Muridae >Gerbillinae<				
<i>Desmodillus auricularis</i> (A. Smith, 1834)	10	9.17	3	1.49
<i>Gerbillurus vullinus</i> (Thomas, 1918)	80	73.39	44	21.78
<i>Gerbillurus paeba</i> (A. Smith, 1836)	1	0.92		
<i>Tatera leucogaster</i> (Peters, 1852)			118	58.42
>Murinae<				
<i>Aethomys namaquensis</i> (A. Smith, 1834)	1	0.92	13	6.44
<i>Mus indutus</i> (Thomas, 1910)			2	0.99
<i>Rhodomys pumilio</i> (Sparrman, 1784)	12	11.01	4	1.98
<i>Saccostomus campestris</i> (Peters, 1946)	4	3.67	9	4.46
total individuals	109		202	
Σ captures	282		629	

The overall species richness and abundance was lower in Nabaos than in Gellap-Ost, which is also expressed by the diversity index (Hs) : Nabaos (Hs 0.95; 7 species, 108 individuals.), Gellap-Ost (Hs 1.29; 8 species, 203 individuals). The main species were the gerbils, *Gerbillurus vullinus* (Thomas, 1918) and *Tatera leucogaster* (Peters, 1852). It was striking, that *T. leucogaster* was not recorded on the Nabaos plot. *Mus indutus* (Thomas, 1910) was only trapped in Gellap-Ost, but was also observed once in Nabaos. *Crocidura sp.* was found in owl pellets of *Bubo africanus*, collected in the farming area of Gellap-Ost during the study period, (pers. communication MIKE GRIFFIN, Namibia 2003).

Abundance and diversity

In Nabaos, species diversity and total abundance (3-29 individuals/2ha) was lower than in Gellap-Ost (12-75 individuals/2ha). In both plots, the highest recruitment was found in August 2002 due to the high reproduction activity during the rainy season, followed by decrease of total abundance in October 2002. *G. vullinus* was the dominant species in Nabaos, and only subdominant in Gellap-Ost, where population density fluctuated highly (Fig. 2).

T. leucogaster was the dominant species in Gellap-Ost, with a composition of 33-72% of the total abundance (Fig. 2b). In August 2003, when the abundance of *T. leucogaster* was lowest, the proportion of other species was highest, which is also shown by a high diversity index (1.47). Although fewer species were recorded per trapping session in Nabaos (Fig. 2) compared to Gellap-Ost, there was an overlap in the species occurring in the two plots (Table 1).

Settlement and survival

Considering all individuals which had been trapped at least over 2 trapping sessions (≥ 11 weeks), we found a lower overall recapture rate in Nabaos (19.3%, n=109) than in Gellap-Ost (31.8%, n=198). Five species were recaptured in Gellap-Ost. These were *T. leucogaster* (37.9%), *G. vullinus* (11.4%), *Aethomys namaquensis* (38.5%), *Elephantulus intufi* (66.7%), *Saccostomus campestris* (33.3%). In Nabaos only *G. vullinus* (22.5%) and *Desmodillus auricularis* (20.0%) were recaptured.

The mean minimum 'survival' rate in weeks (w) shows the longest survival period for *E. intufi* in Gellap-Ost (mean 20.0 w, range 1-64 w, n=9), followed by *A. namaquensis* (mean 9.6 w, range 1-41 w, n=13), *T. leu-*

cogaster (mean 8.5 w, range 1-53 w, n=116), *S. campestris* (mean 4.3 w, range 1-11 w, n=9), *G. vallisus* (mean 3.6 w, range 1-42 w, n=44). In Nabaos *G. vallisus* has 'survived' longer (mean 5.5 w, range 1-44 w, n=80) than in Gellap-Ost, but *D. auricularis* was recorded for only the mean of 3.0 weeks (range 1-10 w, n=11). In total ten individuals had been trapped over a period of >40 weeks: two specimens of *G. vallisus* in Nabaos and one in Gellap-Ost, six specimens of *T. leucogaster* (one female 53 weeks) and one male *E. intufi*, which was still trapped in the last trapping session in Gellap-Ost after a 'survival' of about 64 weeks.

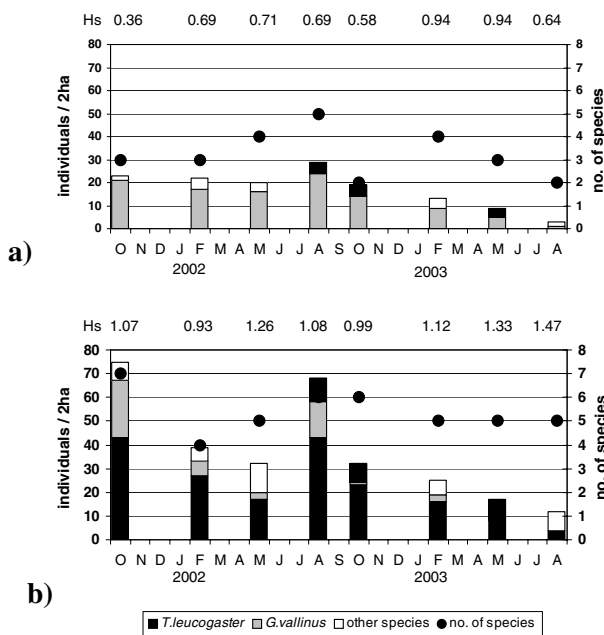


Fig. 2. – a, b: Abundance and diversity of small mammals in neighbouring study sites.

a: Nabaos, **b:** Gellap-Ost. Pictured is the abundance of *G. vallisus* and *T. leucogaster* and other species (pooled), the species number and the Shannon-Wiener-diversity-index for each trapping session.

DISCUSSION

In this study the intensive and uncontrolled grazing by livestock in the communal area had a clear negative impact on species richness, diversity and settlement/survival of small mammals. This suggests that the total loss of ground vegetation cover leads to a reduced food supply (plants, arthropods) and available dew for small mammals. Also disruption of habitat structure, cover and shelter leads to a higher predation risk. Bushes represent areas of high food density and low predation risk (KOTLER, 1984). It is assumed that the decrease of large bushes in the communal area due to the intensive browsing by goats also reduces protection from predation. Burrows in the overgrazed area were found exclusively in bushes, which is probably because of the loss of ground cover, and the direct disturbance by livestock. Intensive and continuous trampling by ungulates is described as a disruptive factor to small mammals (KEESING, 1998; HOFFMANN, 1999; KEESING & CRAWFORD, 2001). Altricial species are much

more sensitive to habitat disturbance. Their requirements in the microhabitat in relation to their nest building behaviour are much higher than for precocial species (ZELLER, 2003).

Many small mammal species are able to successfully tolerate and exploit changes in their physical and biological environments (DELANY & HAPPOLD, 1979). Grazing is one example for such an environmental change, which influences stratification of grass, plant species composition and the standing crop biomass of grassland ecosystems (BOWLAND & PERRIN, 1989). The variety and abundance of small mammal communities might be dependent on how grazers have utilized the grassland (GRANT et al., 1982). Overgrazing affects the food (LACK, 1954) and shelter of small mammals (BOWLAND & PERRIN, 1989). The reduction of vegetation cover exposes them to predation (PEARSON, 1971). NYAKO-LARTEY & BAXTER (1995) found that sites under rotation farming, such as the governmental area in Gellap-Ost, and those grazed by cattle, support more rodents than constantly grazed areas and those grazed by sheep. Therefore it is assumed that the habitat differences across the fence-line is not only caused by the intensity of grazing, but also by the differences in feeding behaviour of goats (primarily browsers) and sheep (selective grazers).

In contrast to a study in the Succulent Karoo (JOUBERT & RYAN, 1999), the small mammal composition in the overgrazed area of Nabaos was never just a subset of the species composition encountered in the moderately grazed areas of Gellap-Ost. Nevertheless, a high overlap of occurring species was found in the year round study. The mean species richness recorded in Nabaos was low (3.3), although it is comparable to the species richness (3.8) recorded in the semi-arid Karoo of southern Africa (KERLEY, 1992b) and in different Fynbos habitats in South Africa (BOND et al., 1980; NEL et al., 1980; ELS & KERLEY, 1996). Species richness was much higher in the lightly grazed area of Gellap-Ost (mean: 5.4 species) across the fence-line. The dominance of small mammal communities also varied. The total disappearance of *T. leucogaster* in the overgrazed area and the dominance of *G. vallisus* was conspicuous. The higher 'survival' rate of *G. vallisus* indicates that this xeric adapted species, which is confined to the western sector of the South West Arid Zone and is known to prefer surface sand (DEGRAAFF, 1981; DEMPSTER et al., 1999), found a more suitable habitat in the degraded land than in the grassy area of Gellap-Ost. This confirms the results of a biodiversity study in rangelands of South Africa (FABRICIUS et al., 2003), where the communal grazing area was characterized by xeric adapted reptiles and predatory arthropods, whereas the nature reserve and commercial farms supported more mesic-adapted species. In contrast, *T. leucogaster* is found in a wide range of savannas and open woodlands of southern Africa (DEGRAAFF, 1981; SMITHERS, 1983), where they generally occur in areas with mean annual rainfall of 250 mm and upwards (SKINNER & SMITHERS, 1990). This gerbil occurs in drier areas like the Nama Karoo where it is assumed to depend on an adequate ground vegetation layer not only because of food availability and cover, but also due to dew water availability. CHRISTIAN (1980) assumes that water availability may play an important role in coexistence and resource alloca-

tion in desert rodents. Because *T. leucogaster* were found to be omnivorous (PERRIN & SWANEPOEL, 1987; NEAL, 1991; MONADJEM, 1997) with a high proportion of plant items like seeds, rhizomes and bulblets (DEGRAAFF, 1981), might also explain their exclusive presence in Gellap-Ost.

Several workers in southern Africa have reported correlations between the distributions of individual small mammal species and measured habitat parameters, especially ground cover (BOND et al., 1980; KERLEY, 1992b; MONADJEM, 1997). The quantity of cover is of prime importance to the density and diversity of small mammals, but when cover reaches threshold levels the degree of plant species diversity becomes important (BOWLAND & PERRIN, 1989). A number of studies have shown that small mammal community structure is a function of plant architecture (ROSENZWEIG & WINAKUR, 1969; BOND et al., 1980; KERLEY, 1992b; ELS & KERLEY, 1996). BOND et al. (1980) and ELS & KERLEY (1996) maintain that microhabitat features such as vegetation structure, cover and height, relative humidity, litter depth, and foliage height diversity are directly related to the life form and growth pattern of plant species within a plant community and these factors are important floristic variables affecting small mammal community structure. The mechanism for this relationship is generally thought to be that niche availability (more specifically foraging microhabitat availability) is a function of habitat complexity: a more complex habitat will contain more niches which may be exploited by more species (ROSENZWEIG & WINAKUR, 1969).

Until now small African mammals have not enough considered adequately in both the planning and management of conservation areas, largely due to the difficulty in assessing this group. According to AVENANT (2000), biodiversity of small mammals can be used as an indicator of disturbance in an ecosystem, whereas the domination of an indicator species, low species richness and low diversity are useful tools for indicating disturbance on the primary producer level. An understanding of determinants of small mammal community structure is therefore important for practical development of arid and semi-arid rangeland management guidelines (KERLEY, 1992b). BARNARD et al., (1998) ascertains that the establishment of wildlife conservation in commercial and communal farmlands could improve the current protection status of the Nama Karoo, with rural communities responsible for the ecological management of large areas in habitats otherwise overlooked for conservation.

ACKNOWLEDGEMENTS

The study was carried out in the framework of the BIOTA project financed by BMBF. We appreciate the support of the Ministry of Environment and Tourism of Namibia, National Museum of Namibia, the Gellap-Ost Research Station and the village people from Nabaoos. We wish to thank Mike Griffin for his valuable advices and for the analysis of the owl pellets. We thank Seth Eiseb, Walter Hauwanga, Erik Maluleke and Mathew Shuyua for their excellent field assistance. We are grateful to Katrin Vohland for providing her entomological expertise.

REFERENCES

- ABRAMSKY, Z. (1988). The role of habitat and productivity in structuring desert rodent communities. *Oikos*, 52 : 107-114.
- AVENANT, N.L. (2000). Small mammal community characteristics as indicators of ecological disturbance in Willem Pretorius Nature Reserve, Free State, South Africa. *South African Journal of Wildlife Research*, 30 (1) : 26-33.
- BARNARD, P., C.J. BROWN, A.M. JARVIS, A. ROBERTSON & L. VAN ROOYEN (1998). Extending the Namibian protected area network to safeguard hotspots of endemism and diversity. *Biodiversity and Conservation*, 7 : 531-547.
- BOND, W., M. FERGUSON & G. FORSYTH (1980). Small mammals and habitat structure along altitudinal gradients in the southern Cape mountains. *South African Journal of Zoology*, 15 : 34-43.
- BOWLAND, A.E. & M.R. PERRIN (1989). The effect of overgrazing on small mammals in Umfolozi Game Reserve. *Zeitschrift für Säugetierkunde*, 54 : 251-260.
- BRONNER, G. & J. MEESTER (1987). Comparison of methods for estimating rodent numbers. *South African Journal of Wildlife Research*, 17 (2) : 59-63.
- CHRISTIAN, D.P. (1980). Vegetative cover, water resources, and microdistributional patterns in a desert rodent community. *Journal of Animal Ecology*, 49 : 807-816.
- COWLING, R.M. (1986). A description of the Karoo Biome Project. *South African National Scientific Programmes Report 122*, Pretoria.
- DeGraaff, G. (1981). *The rodents of Southern Africa*. Durban, Butterworths.
- DEAN, W.R.J. & S.J. MILTON (1995). Plant and invertebrate assemblages on old fields in the arid southern Karoo, South Africa. *African Journal Ecology*, 33 : 1-13.
- DEAN, W.R.J. & S.J. MILTON (1999). *The Karoo. Ecological patterns and processes*. Cambridge University Press, Cambridge.
- DELANY, M.J. (1964). An ecological study of the small mammals in the Queen Elizabeth Park, Uganda. *Revue de Zoologie et de Botanique Africaines*, 70 (1-2) : 129-147.
- DELANY, M.J. & D.C.D. HAPPOLD (1979). *Ecology of African mammals*. Longman, London and New York, 434pp.
- DEMPSTER, E.R., M.R. PERRIN & C.T. DOWNS (1999). *Gerbillus vullinus*. *Mammalian Species*, 605 : 1-4.
- ELS, L.M. & G.I.H. KERLEY (1996). Biotic and abiotic correlates of small mammal community structure in the Groendal Wilderness Area, Eastern Cape, South Africa. *Koedoe*, 39 (2) : 121-130.
- FABRICIUS, C., M. BURGER & P.A.R. HOCKEY (2003). Comparing biodiversity between protected areas and adjacent rangeland in xeric succulent thicket, South Africa: arthropods and reptiles. *Journal of Applied Ecology*, 40 : 392-403.
- GRANT, W.E., E.C. BIRNEY, N.R. FRENCH & D.M. SWIFT (1982). Structure and productivity of grassland small mammal communities related to grazing-induced changes in vegetative cover. *Journal of Mammalogy*, 63 : 248-260.
- HOFFMAN, M.T., B. COUSINS, T. MEYER, A. PETERSEN & H. HENDRIKS (1999). Historical and contemporary agricultural land use and the desertification of the Karoo. In : DEAN, W.R.J. & S.J. MILTON (eds), *The Karoo. Ecological patterns and processes*, Cambridge University Press, Cambridge : 257-273.
- HOFFMANN, A. (1999). *Habitatnutzung und Populationsdynamik von Kleinsäugetern im Grasland des Queen Elizabeth National Park, Uganda*. Dissertation, Technische Universität Braunschweig, (<http://www.biblio.tubs.de/ediss/data/20000114a/20000114a.html>).
- HOFFMANN, A., K. VOHLAND, P. GIERS & U. ZELLER (2003). Influence of grazing intensity on biodiversity of small mammals and arthropods in the Nama Karoo of southern

- Namibia. Abstract. In : *Arid Zone Ecology Forum Conference 2003*, Kathu, South Africa.
- HUGHES, J.J., D. WARD & M.R. PERRIN (1994). Predation risk and competition affect habitat selection and activity of Namib desert gerbils. *Ecology*, 75 (5) : 1397-1405.
- HUGO, A. (1990). Wiederfangerfolg bei Kleinsäugetern mit einer neuen Markierungsmethode. *Zeitschrift für Säugetierkunde*, 55 : 421-424.
- JOUBERT, D.F. & P.G. RYAN (1999). Differences in mammal and bird assemblages between commercial and communal rangelands in the Succulent Karoo, South Africa. *Journal of Arid Environment*, 43 : 287-299.
- KEESING, F. (1998). Ecology and behavior of the pouched mouse, *Saccostomus mearnsi*, in central Kenya. *Journal of Mammalogy*, 79 (3) : 919-931.
- KEESING, F. & T. CRAWFORD (2001). Impacts of density and large mammals on space use by the pouched mouse (*Saccostomus mearnsi*) in central Kenya. *Journal of Tropical Ecology*, 17 : 464-472.
- KERLEY, G.I.H. (1992a). Small mammal seed consumption in the Karoo, South Africa : further evidence for divergence in desert biotic processes. *Oecologia*, 89 : 471-475.
- KERLEY, G.I.H. (1992b). Ecological correlates of small mammal community structure in the semi-arid Karoo, South Africa. *Journal of Zoology, London*, 227 : 17-27.
- KOTLER, B.P. (1984). Risk of predation and the structure of desert rodent communities. *Ecology*, 65 : 689-701.
- LACK, D. (1954). *The natural regulation of animal numbers*. Oxford, Clarendon Press.
- LLOYD, J.W. (1999). Nama Karoo. In : J. KNOBEL (ed), *The magnificent natural heritage of South Africa*, Sunbird Publishing, Cape Town, South Africa : 84-93.
- LONDO, G. (1975). De decimale schaal voor vegetatiekundige opnamen van permanente Kwadranten. *Gorteria*, 7 (7) : 101-106.
- LOVEGROVE, B. (1993). *The living deserts of southern Africa*. Fernwood Press, Cape Town.
- MENDELSON, J., C. ROBERTS & T. ROBERTSON (2002). *Atlas of Namibia. A portrait of the land and its people*. Publisher : Ministry of environment and Tourism of Namibia, Cape Town.
- MONADIEM, A. (1997). Habitat preferences and biomasses of small mammals in Swaziland. *African Journal of Ecology*, 35 : 64-72.
- MONADIEM, A. (1999). Population dynamics of *Mus minutoides* and *Steatomys pratensis* (Muridae : Rodentia) in a subtropical grassland in Swaziland. *African Journal of Ecology*, 37 : 202-210.
- NEAL, B.R. (1991). Seasonal changes in reproduction and diet of the Bushveld gerbil, *Tatera leucogaster* (Muridae : Rodentia), in Zimbabwe. *Zeitschrift für Säugetierkunde*, 56 : 101-111.
- NEL, J.A.J., I.L. RAUTENBACH & G.J. BREYTENBACH (1980). Mammals of the Kammanassie Mountains, southern Cape Province. *South African Journal of Zoology*, 15 : 255-261.
- NOY-MEIR, I., M. GUTMAN & Y. KAPLAN (1989). Responses of Mediterranean grassland plants to grazing and protection. *Journal of Ecology*, 77 : 290-310.
- NYAKO-LARTEY, Q. & R.M. BAXTER (1995). The effects of different grazing regimes on the population dynamics of small mammals in the Eastern Cape. *Transvaal Royal Society of South Africa*, 50 (2) : 143-151.
- OLSVIG-WHITTAKER, L.S., P.E. HOSTEN, I. MARCUS & E. SHOCHAT (1993). Influence of grazing on sand field vegetation in the Negev Desert. *Journal of Arid Environment*, 24 : 81-93.
- PEARSON, O.P. (1971). Additional measurements of the impact of carnivores on California voles (*Microtus californicus*). *Journal of Mammalogy*, 52 : 41-49.
- PERRIN, M.R. & P. SWANEPOEL (1987). Breeding biology of the bushveld gerbil *Tatera leucogaster* in relation to diet, rainfall and life history theory. *South African Journal of Zoology*, 22 (3) : 218-227.
- PRICE, M.V. & S.H. JENKINS (1986). Rodents as seed consumers and dispersers. In : MURRAY, D.R. (ed), *Seed dispersal*, Academic Press, Australia : 191-235.
- RIVERS-MOORE, N.A. & M.J. SAMWAYS (1996). Game and cattle trampling, and impact of human dwellings on arthropods at a game park boundary. *Biodiversity and Conservation*, 5 : 1545-1556.
- ROSENZWEIG, M.L. & J. WINAKUR (1969). Population ecology of desert rodent communities : habitats and environmental complexity. *Ecology*, 50 (4) : 558-572.
- ROWE-ROWE, D.T. & T. MEESTER (1982). Habitat preferences and abundance relations of small mammals in Natal Drakensberg. *South African Journal of Zoology*, 17 : 202-209.
- SEYMOUR, C.L. & W.R.J. DEAN (1999). Effects of heavy grazing on invertebrate assemblages in the Succulent Karoo, South Africa. *Journal of Arid Environment*, 43 : 267-286.
- SKINNER, J.D. & R.H.N. SMITHERS (1990). *The mammals of the southern African subregion*. Pretoria, University of Pretoria.
- SMITHERS, R.H.N. (1983). *The mammals of the southern African subregion*. Pretoria, University of Pretoria.
- TODD, S.W. & M.T. HOFFMAN (1999). A fence-line contrast reveals effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. *Plant Ecology*, 142 : 169-178.
- VENTER, J.M., C. MOCKE & J.M. DE JAGER (1986). Climate. In : CROWLING, R.M., P.W. ROUX & A.J.H. PIETERSE (eds), *The Karoo Biome : a preliminary synthesis. Part 1. Physical Environment*. South African National Scientific Programmes Report 124, Pretoria.
- VOHLAND, K., M. UHLIG, E. MARAIS, A. HOFFMANN & U. ZELLER (2005). Impact of different grazing systems on diversity, abundance and biomass of beetles (Coleoptera), a study from Southern Namibia. *Mitteilungen aus dem Museum für Naturkunde in Berlin, Zoologische Reihe*, 81 (2) : 131-143.
- ZELLER, U. (2003). Functional zooidiversity in biomes of southern Africa and its changes by land-use and environment. In : *BIOTA Southern Africa. Towards sustainable use of biodiversity*. Published by University of Hamburg, Botanical Institute and Botanical Garden, Volume I : 231-264.