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The impact of overgrazing on reptile diversity and population dynamics of *Pedioplanis l. lineoocellata* in the southern Kalahari

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Impact of overgrazing on reptile diversity and population dynamics of *Pedioplanis l. lineoocellata* in the southern Kalahari, South Africa

**Dissertation
zur Erlangung des akademischen Grades
"doctor rerum naturalium"
(Dr. rer. nat.)
in der Wissenschaftsdisziplin " Ökologie"**

**eingereicht an der
Mathematisch-Naturwissenschaftlichen Fakultät
der Universität Potsdam**

**von
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Potsdam, den 31.08.2007

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Preface

The aim of my PhD-thesis is to analyse the impact of overgrazing caused by intensive land use on the reptile community in the southern Kalahari and to understand the effect of changing habitats on population dynamics of the lizard *Pedioplanis lineoocellata lineoocellata*. My thesis consists of four major chapters which can be read independently, since every single chapter focus on a specific part of the influence of overgrazing on reptiles. Owing to the cumulative form of my thesis, some parts (e.g. methods) overlap to some extent. The first three chapters are submitted to scientific journals in cooperation with co-authors and the fourth chapter is in preparation. Because of the idea to submit all chapters to scientific journals my thesis has been written in the first person plural. Co-authors include my thesis advisor Prof. Dr. Florian Jeltsch, my thesis co-advisor Dr. Joh Henschel and Dr. Niels Blaum, who has been partners of fruitful discussion. Nonetheless, all findings presented here resulted from work that has been done independently by me.

General Introduction

In semi-arid and arid savannah ecosystems, the vegetation structure and composition, i.e. the architecture of trees, shrubs, grass tussocks and herbaceous plants, offer a great variety of habitats and niches to sustain animal diversity. However, in the last decades intensive human land use practises like livestock or game farming have altered the vegetation composition and structure in savannah ecosystems worldwide (Roques et al. 2001, Sankaran et al. 2005). One of the most threatening forms of vegetation change is shrub encroachment caused by overgrazing. Extensive grazing leads to a reduction of the perennial and herbaceous vegetation cover (Jeltsch et al. 1997, Van Auken 2002, Wiegand et al. 2005), which results in an increased availability of bare soil (Skarpe, 1990). Both, the missing competition with perennial grasses and the increase of bare soils favour shrub establishment (Teague and Smit, 1992; Jeltsch et al., 1997) on open ground and lead to area-wide shrub encroachment or even desertification (Skarpe 1990, Teague and Smit 1992, Jeltsch et al. 1997).

Jeltsch F, Milton SJ, Dean WRJ, Van Rooyen N (1997) Analysing shrub encroachment in the southern Kalahari: a grid-based modelling approach. Journal of Applied Ecology 34, 1497-1508

Roques KG, O'Connor TG, Watkinson AR (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. Journal of Applied Ecology 38, 268-280

Sankaran M, Hanan NP, Scholes RJ, Ratnam J, Augustine DJ, Cade BS, Gignoux J, HIGGINS SI, Le Roux X, Ludwig F, Ardo J, Banyikwa F, Bronn A, Bucini G, Caylor KK, Coughenour MB, Diouf A, Ekaya W, Feral CJ, February EC, Frost PGH, Hiernaux P, Hrabar H, Metzger KL, Prins HHT, Ringrose S, Sea W, Tews J, Worden J, Zambatis N (2005) Determinants of woody cover in African savannas. Nature 438, 846-849

Skarpe C (1990) Structure of the woody vegetation in disturbed and undisturbed arid savanna, Botswana. Vegetatio 87, 11-18

Teague WR, Smit GN (1992) Relations between woody and herbaceous components and the effects of bush-clearing in the southern African savanna. Journal of the Grassland Society of South Africa 9, 60-71

Van Auken OW (2000) Shrub Invasion of North American Semiarid Grasslands. Annual Revue of Ecological Systems 31, 197-215

Wiegand K, Ward D, Saltz D (2005) Multi-scale Patterns and Bush Encroachment in an Arid Savanna With a Shallow Soil Layer. Journal of Vegetation Science311-320

As a consequence of the altered vegetation structure and composition, the structural diversity declines (Tews et al. 2004) which can lead to habitat degradation, fragmentation and loss. It has been shown that with decreasing structural diversity animal diversity decline across a variety of taxa (e.g. Dennis et al. 1998, Meik et al. 2002) (Figure 1).

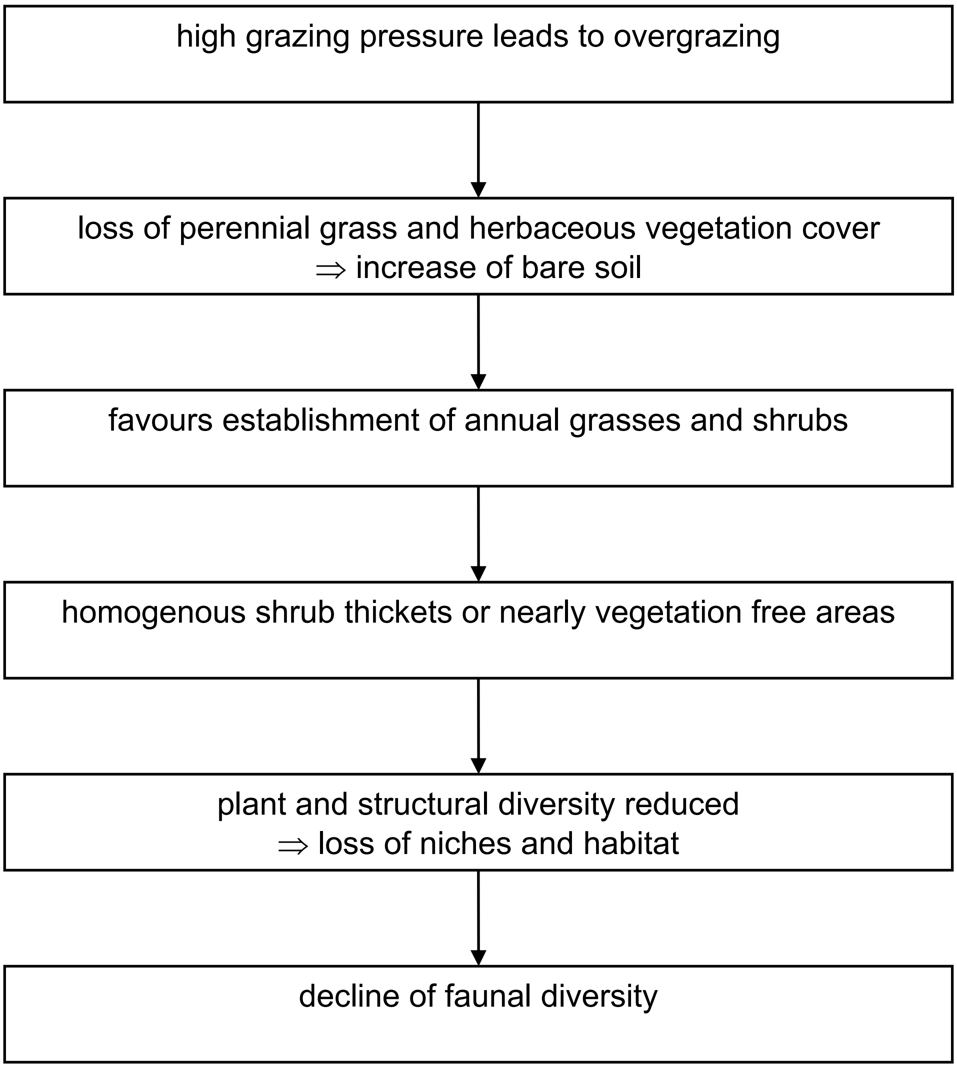

Figure 1 course and effects of overgrazing

Dennis P, Young MR, Gordon IJ (1998) Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. Ecological Entomology 23, 253-264

Meik JM, Jeo RM, Mendelsson III JR, Jenks KE (2002) Effects of bush encroachment on an assemblage of diurnal lizard species in central Namibia. Biological Conservation 106, 29-36

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity of the vegetation: the importance of keystone structures. Journal of Biogeography 31, 1-14

The Kalahari is one of the largest arid savannah systems of the world. Here, large areas suffer from habitat degradation caused by anthropogenic land use. However, while the impact of habitat degradation on plant diversity is relatively well studied (e.g. Skarpe 1990, Floyd et al. 2003), knowledge on how overgrazing affects animal diversity remain sparse. Especially, data on the effects of overgrazing on reptiles, which are an important part of the ecosystem, are missing. Furthermore, the impact of habitat degradation on factors of a species population dynamic and life history, e.g., birth rate, survival rate, predation risk, space requirements or behavioural adaptations are poorly known.

Therefore, one aim of my PhD-thesis is to analyse the impact of overgrazing caused by intensive land use on the reptile community in the southern Kalahari. However, to really predict the long term consequences of habitat degradation for animal diversity, one has to understand the effect of changing habitats on population dynamics of reptiles. Therefore, the second aim of my PhD-thesis is to investigate population dynamics and behaviour of one reptile species in particular. As a model species, I chose the most common species, the Spotted Sand Lizard, *Pedioplanis lineoocellata lineoocellata* (Figure 2).

Figure 2 Pedioplanis l. lineoocellata

Floyd LM, Fleischner TL, Hanna D, Whitefield P (2003) Effects of Historic Livestock Grazing on Vegetation at Chaco Culture National Historic Park, New Mexico. Conservation Biology 17, 1703-1711

Skarpe C (1991) Impact of grazing in savanna ecosystems. Ambio 20, 351-356

Reptiles are regularly used as model systems in ecology (Huey et al. 1983, Vitt and Pianka 1994). As they rarely engage in social behaviours such as parental activities (Somma 1990) and usually don't live in well-defined social groups complications that emerge in studies which concentrate on social animals are avoided. Data on the influence of environmental factors on reptile diversity and population dynamics are more precisely and clearly to interpret because it is not necessary to distinguish between the effects caused by environmental factors and the effects caused by the social system and social behaviour.

The Kalahari (a corruption of the word Kgalagadi; in the Setswana language it means always dry (van Rooyen 2001)) is a vast region that covers an area of 2.5 million square kilometre from the Orange River in the south up to the Congo Basin in the north (Thomas and Shaw 1993; Knight and Joyce 1997). The field study was conducted from August 2004 to May 2006 in the southern Kalahari savannah rangeland south of the Kgalagadi Transfrontier Park in the Northern Cape Province, South Africa. The southern Kalahari lies in the border-zone of Botswana, Namibia and South Africa. The study area covers approximately 10000 km^2 (N-S: ~110km & W-E ~90km). To investigate the effects of different grazing intensities on reptile diversity I selected 16 privately owned commercial sheep farms which are distributed over the whole area (Figure 3).

Floyd LM, Fleischner TL, Hanna D, Whitefield P (2003) Effects of Historic Livestock Grazing on Vegetation at Chaco Culture National Historic Park, New Mexico. Conservation Biology 17, 1703-1711

Huey RB, Pianka ER, Schoener TW (1983) Lizard ecology: studies of a model organism. Havard University Press, Cambridge, Massachusetts

Knight M, Joyce P (1997) The Kalahari: Survival in a thirstland wilderness.

Somma LA (1990) A categorization and bibliographic survey of parental behavior in lepidosaurian reptiles. Smithsonian Herpetological Information Service 81, 1-53

Van Rooyen N. (2001) Flowering plants of the Kalahari dunes.

Vitt LJ, Pianka ER (1994) Lizard ecology: historical and experimental perspectives. Princeton University Press, Princeton, New Jersey

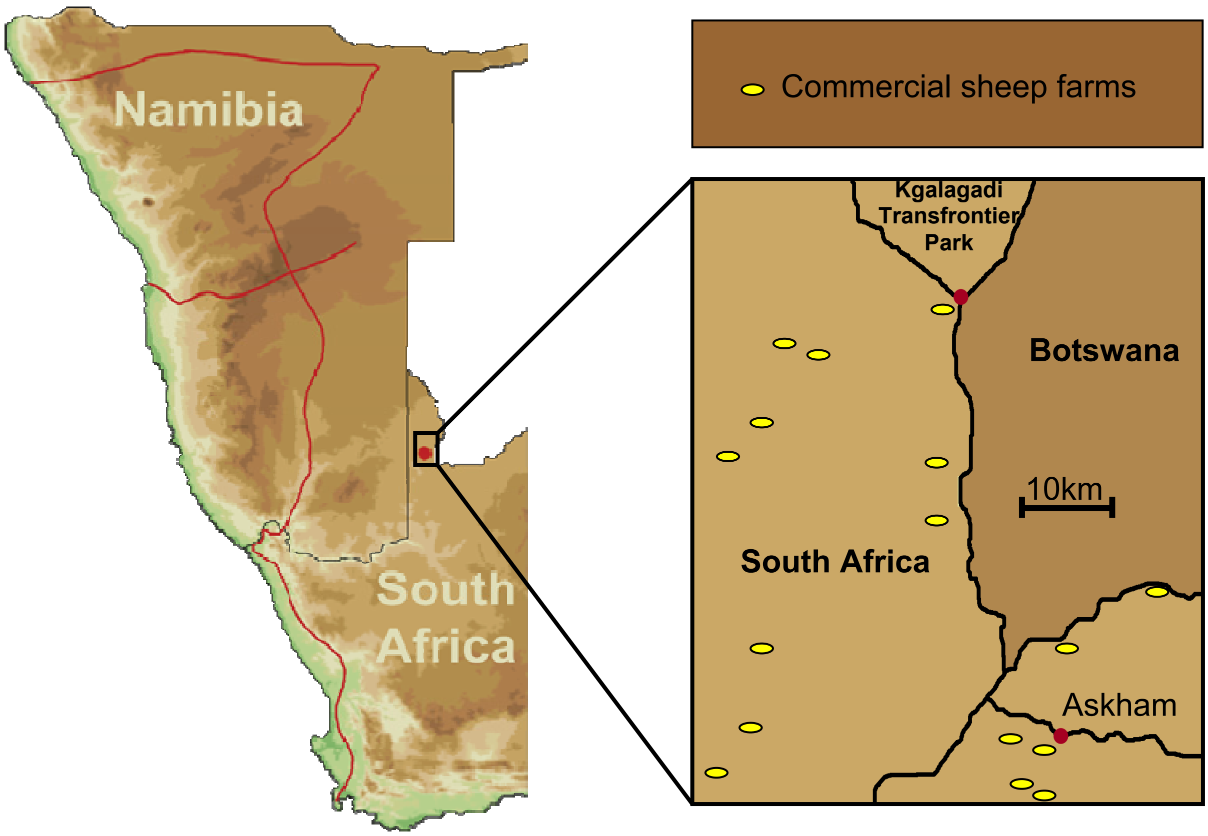

Figure 3 Map of research area and study sites

With my investigations I will demonstrate (i) that habitat degradation has serve negative impacts on the reptile community and (ii) that it is of importance to investigate not only the response of the whole community to habitat degradation but also aspects of a species life history and its population dynamics.

Outlines of the thesis

This thesis is based on four chapters. Each of the four chapters can be read independently. To obtain an overview over the reptile situation in general I investigated in chapter one the impact of overgrazing on the reptile community on the regional scale in the southern Kalahari, South Africa. In the following three chapters I concentrated on one species, the Spotted Sand Lizard, *Pedioplanis l. lineoocellata* to gain a deeper understanding of major parts of an animal’s life history. In chapter two behavioural adaptations of *P. lineoocellata* to habitat degradation were examined. The space use of *P. lineoocellata* in dependence of habitat degradation was studied in chapter three. In the fourth and last chapter I examined the influence of habitat degradation on several traits of the species, namely absolute population size, survival rate, birth rate and fitness. At the end I give a summary discussion, where I interlink the results of the preceding chapters followed by a summary in German. Please not the introductory words concerning the composition of this thesis in the preface after the table of contents.

Chapter 1

Effects of habitat degradation on regional reptile diversity

Psammobates oculiferus

Chondrodactylus a. angulifer

Nucras tessellata (juvenile)

Effects of habitat degradation on regional reptile diversity[1]

1. Abstract

In a three year Visual Encounter study (VES) we investigated the impact of habitat degradation on regional reptile diversity and abundance along a grazing gradient in the southern Kalahari, South Africa. We distinguished five different vegetation states from high perennial grass cover and low shrub cover to low perennial grass and high shrub cover. Our results, not affected by short term climatic conditions, time or area, showed that reptile abundance of single species and the community as a whole decline with increasing shrub cover and loss of perennial grasses. Also reptile diversity decreases with habitat degradation. An increase of predation risk, a decrease of resource availability (prey) and reduced possibilities to thermoregulate may have resulted in lower reptile abundance and diversity in degraded habitats. Hence, habitat degradation caused by overgrazing has a serve negative impact on reptile abundance and diversity in semiarid rangelands.

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[1] This chapter is submitted as:
Wasiolka B., Blaum N., Henschel J. and Jeltsch, F.: Effects of habitat degradation on regional reptile diversity. Biodiversity and Conservation

2. Introduction

In savannah ecosystems, vegetation structures i.e. architecture of trees, shrubs, grass tussocks and herbaceous plants offer a great variety of niches and microhabitats crucial to sustain animal diversity (Lawton 1983; Price 1986; Dean et al. 1999; Tews et al. 2004). This structural diversity (Tews et al. 2004) is modified by heavy grazing of domestic livestock which can lead to area wide shrub encroachment (e.g. Skarpe 1990b; Teague and Smit 1992; Jeltsch et al. 1997) at the cost of perennial and herbaceous vegetation cover (e.g. Jeltsch et al. 1996; Van Auken 2000, Wiegand et al. 2005). This structural change of savannah vegetation occurs worldwide (e.g. Archer et al. 1988, O'Connor 1995, Roques et al. 2001) and reduces habitat heterogeneity at different spatial scales (Blaum et al. 2006, Manning et al. 2006). Shrub encroachment thus leads to habitat loss and habitat fragmentation which is thought to reduce plant and animal species diversity (Mac Arthur 1965; Tews et al. 2004; Blaum et al. 2006).

Whereas the impact of overgrazing on plant diversity is relatively well studied (e.g. Skarpe 1990a, Floyd et al. 2003), knowledge how overgrazing affects animal diversity remain sparse. Changes in vegetation structure, composition and cover caused by overgrazing can alter environmental conditions such as the availability of resources (Saunders et al. 1991) or cover (safe sites) (Huey and Pianka 1981) for a variety of species. Negative effects of this change have been documented for mammals (Blaum et al. 2006, Blaum et al. 2007) or birds (Pianka and Huey 1971) in the southern Kalahari. However, the influence of decreasing habitat diversity and quality is yet not well investigated for reptiles. Reptiles stand at the beginning of the food chain and thus make ideal study objects to detect early changes in diversity and abundance. Hence, they are likely to react immediately to alterations in vegetation states. In addition to direct negative effects of structural changes in the habitat (i.e. the relative cover of shrubs and herbaceous vegetation), reptile diversity can be negatively affected by a decline of invertebrate abundance, the main prey source for most of the reptile species in the Kalahari (Pianka 1986). Invertebrate decline is typically caused by reduction of perennial grass cover (Gandar 1982; Dennis et al. 1998; Seymour and Dean 1999).

To gain a better understanding of the effects of overgrazing and resulting shrub encroachment on population dynamics and diversity of animals it is crucial to include a regional scale perspective (Levin 1992, Shurin et al. 2000, Leibold et al. 2004). Only regional scale studies comprise relevant mechanisms such as e.g. dispersal, metapopulation or sink source dynamics (Hanski 1998, Boughton 1999, Hanski and Ovaskainen 2003). In a three year field study we conducted standardized Visual Encounter Surveys on the regional scale to obtain information on abundance (single species and the whole community) and diversity of reptiles across a gradient of grazed habitats ranging from vegetation state 1 (highest habitat diversity/quality, lowest grazing impact) to vegetation state 5 (lowest habitat diversity/quality, highest grazing impact). We addressed the following hypotheses: (1) Reptile abundance and diversity decreases with habitat degradation; (2) Invertebrate abundance decreases with habitat degradation; (3) As a consequence of serve vegetation alteration even generalist reptile species which utilize a wide range of different habitats show preference for habitats of high habitat diversity.

3. Methods

3.1 Study Area and Period

The study was conducted from September 2004 to February 2006 in the southern Kalahari savannah rangeland south of the Kgalagadi Transfrontier Park in the Northern Cape Province, South Africa. The study area covers approximately 10000 km^2 (N-S: ~110km & W-E ~90km). To investigate the effects of different grazing intensities on reptile diversity we selected sixteen privately owned commercial sheep farms (Abbas (S 26°30’; E 20°35’), Bloukranz (S 26°52’; E 20°21’), Branduin No. 61 (S 26°32’; E 20°26’), Branduin No. 62 (S 26°37’; E 20°33’), Hoekrans (S 26°39’, E 20°34’), Inversnaid (S 26°55’; E 20°46’), Kastraat (S 26°38’; E 20°24’), Linlithgow (S 27°09’; E 20°29’), Loch Lemond (S 27°03’; E 020°45’), Loch Maree (S 27°06’; E 20°20’), Rappels (S 26°49’; E 20°51’), Rea (S 27°01’,E 20°40’), Rooiduin (S 26°42’; E20°35’), Swartpan (27°15’; E20°46’), Valsvlei No. 71 (S 26°41’; E 20°19’) and Vry Soutpan (S 27°17; E20°50’)) which are distributed over the whole area.

The savannah vegetation is described as the western form of the Kalahari Thornveld (Acocks 1988) where trees (e.g. *Acacia erioloba, A. haematoxylon and Boscia albitrunca)* and shrubs (e.g. *Grewia flava, Lycium hirsutum, Acacia mellifera* and

Rhigozum trichotomum.) are sparsely scattered in a grassy matrix. The main grass species are *Aristida* ssp. and *Eragrostis* ssp. in the valleys and *Centropodia glauca, Stipagrostis namaquensis, Stipagrostis uniplumis, Monechma incanum* and *Crotalaria virgultalis* on the dunes (Leistner 1959; Pianka and Huey 1971; Acocks 1988). Annual rainfall ranges from 150mm to 300mm (Leistner and Werger 1973) and falls mainly in summer (Werger 1978). Temperature extremes range from winter lows reaching –10.3 °C to summer highs up to 45.4 °C (van Rooyen 2001).

3.2 Reptile Survey

We estimated reptile diversity by time and area constrained Visual Encounter Surveys (VES) (Heyer et al, 1994; Cooper and Whiting, 2000; Meik et al, 2002). Each VES was conducted along transects (30 minutes / 5m x 500m) parallel to the dunes along the valleys. This method allowed us to observe, identify, and count each species and individual. Neighbouring dune valleys consisted of similar vegetation composition. Hence, we minimized edge effects by locating surveys away from habitat boundaries. We investigated five different vegetation states (Table 1) ranging from vegetation state 1 to vegetation state 5. The vegetation states are characterized by different vegetation composition and cover. Grazing intensity increases from vegetation state 1 to vegetation state 5 and structural diversity and habitat quality decreases from state 5 to state 1. These vegetation states were chosen because they represent states generated by low versus high grazing pressure as well as by short versus long term effects (Walker et al. 1981). Vegetation state 1 (low grazing pressure/short term effect) and vegetation state 5 (high grazing pressure/long term effect) are two states at opposite ends of the spectrum (Walker et al., 1981; Skarpe, 1990a,b; Moleele and Perkins, 1998). The three other vegetation states are intermediate states (Walker et al., 1981). We walked four times (Oct. 2004, Jan. 2005, Oct. 2005 & Jan. 2006) 12 transects of each vegetation state, evenly distributed on sixteen farms within the research area (four transects each in the northern, central & southern region). As an exception we walked only eight transects of the vegetation state 5 because no suitable habitats with corresponding vegetation composition were found in the northern parts of the research area.

To minimize observer bias all transects were observed by the same person. Because plots were repeatedly surveyed we minimized the habitat disturbance by including only visible reptiles during the VES, i.e. we avoided moving any cover objects like logs or leaf litter. In sum, a total of 224 transects were surveyed.

3.3 Vegetation Survey

To quantify the differences in habitat characteristics, we sampled the same transects as for the VES of reptile diversity. Twice, during January 2005 and 2006 we surveyed 500m long transects on all five vegetation states. Every 50m on these transects a 4m by 4m square was surveyed. Percent ground cover of all plant species was estimated and the mean of tree-, shrub-, perennial grass-, annual grass- and herbaceous cover calculated. In total we sampled 112 vegetation transects.

3.4 Prey Availability

To assess prey availability we investigated Orthoptera abundance (< 2.5 cm body length), one of the main food sources of reptiles especially during summer (Pianka 1986). During January 2005 and 2006 we surveyed Orthoptera (< 2.5 cm body length) abundance in the same habitats as the VES for reptiles. On each transect of the VES for reptiles we walked four sub-transects (3m x 100m) with inter-transect spacing of 25m where we visually counted all Orthoptera. Each year a total of 224 transects were surveyed.

3.5 Habitat preference

In an additionally analysis we investigated the habitat preference of the three dominating reptile species: *Pedioplanis l. lineoocellata*, *Heliobolus lugubris* and *Mabuya variegata* (Wasiolka 2004). Therefore, we compared available habitat with used habitat for each of the three mentioned reptile species.

3.6 Data Analyses

We calculated abundance (e.g. Steenkamp and Chown, 1995) and species richness (e.g. Gotelli and Colwell, 2001) of reptiles, the Shannon Index (e.g. Shannon, 1948) of vegetation diversity and abundance of Orthoptera. To evaluate abundance (reptiles & Orthoptera), species richness (reptiles) and the Shannon Index (vegetation diversity) as well as abundance of the three dominating reptile species the means were compared. Furthermore, we tested all datasets for variances in regard to variation in seasons (dry vs. rainy season), annual variation (04/05 vs. 05/06) and regional variation (Northern areas vs. central areas vs. southern areas.

We used one-factor ANOVA (Dytham 1999) ((© SPSS Inc., Version 11.5) to analyse the abundance of reptiles and Orthoptera, species richness of reptiles and vegetation diversity. To test for differences between the vegetation states we used a Post-Hoc-Test (Tukey-Test). Seasonal and annual variations were tested with a T-test and regional variations with a one-factor ANOVA.

For the habitat preferences analysis a G-Test (Chi² Log Likelihood test) was applied to test whether distributions of available and used habitats (vegetation states) in the research area were significantly different (Neu et. al, 1974; Zar, 1998). To assess reptile preferences or avoidance of the different habitats we calculated the selection index w_i (Savage 1931).

$w_i = \frac{o_i}{p_i}$; o_i = proportion of lizards in habitat, p_i = proportion of available habitats

Selection indices above 1.0 indicate preferences; values less than 1.0 indicate avoidance. Because w_i can range from 0 to ∞ Manly et al. (1993) suggest presenting a standardized selection index (B_i) that sum to 1.0 for all classes of the resource.

$B_i = \frac{\hat{w}_i}{\sum_{i=1}^{n} \hat{w}_i}$; $\hat{w}_i$ = selection Index

Index values of (1/ number of shrub species) indicate no preference; higher values indicate a preference and lower values indicate a relative avoidance of a vegetation scenario.

To test statistically that any specific resource class was used significantly non-randomly (either avoidance or preference) individual confidence intervals were constructed for each w_i. The selection coefficient w_i is significantly different if the confidence interval for w_i does not contain the value 1 (Krebs 1999). Both index values were calculated by applying "Programs for Ecological Methodology, 2nd ed." (© Krebs 2002) using "Niche Measure – Resource Selection" procedure (Krebs 1999). For all tests P-value of < 0.05 was regarded as statistically significant.

4. Results

4.1 Vegetation Survey

The results of the vegetation survey confirm that the sampled sites can be assigned to five classes of vegetation cover (vegetation states) in terms of shrub cover, perennial grass cover, annual grass cover, herb cover and bare ground (Table 1). Vegetation state 1 and 2 ("non-degraded habitats") displayed significant higher vegetation diversity than areas of vegetation state 3, 4 and 5 ("degraded habitats") (Figure 1).

Table 1 Range of vegetation cover of shrubs, perennial grasses, annual grasses, herb, bare ground and diversity index (H') for the five vegetation states

Vegetation state	Vegetation cover (%)					
	Shrubs	Perennial grass	Annual Grass	Herbs	Bare ground	Diversity Index (H')
vegetation state 1	0-1	31-38	0-1	2-5	57-65	0.72
vegetation state 2	0-1	19-30	4-7	1-5	61-72	0.78
vegetation state 3	13-18	3-9	7-12	0-2	65-76	0.51
vegetation state 4	20-32	1-7	2-11	0-1	58-71	0.31
vegetation state 5	0-1	0-2	19-32	0-1	64-81	0.22

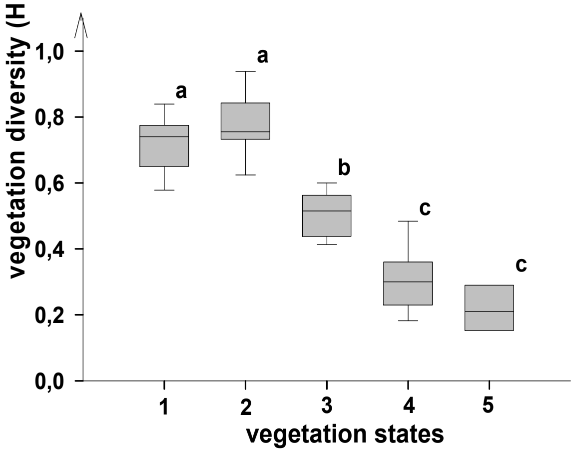

Figure 1 Means ± SE of vegetation diversity for the five vegetation states. Different letters (a, b, c) indicate significant differences between the respective vegetation states (ANOVA, Tukey Post Hoc Test, p-value < 0.05).

4.2 Reptile Survey

Table 2 shows the species inventory for the five vegetation states.

Table 2 Reptile species inventory within the five vegetation states

Species	Vegetation state 1	Vegetation state 2	Vegetation state 3	Vegetation state 4	Vegetation state 5
Pedioplanis l. lineoocellata	x	x	x	x	x
Pedioplanis namaquensis	-	-	x	x	x
Heliobolus lugubris	x	x	x	-	-
Meroles suborbitalis	-	-	-	-	x
Nucras tessellata	-	-	x	-	-
Agama a. aculeata	-	-	x	x	-
Mabuya variegata punctulata	x	x	-	-	-
Mabuya occidentalis	x	-	-	-	
Bitis caudalis	x	x	-	-	-
Psammophis leightoni trinasalis	x	x	-	-	-
Psammobates oculiferus	x	-	-	-	-

X: present
-: absent

We found no significant differences in reptile abundance and diversity between seasons (dry vs. rainy season) (abundance: $F_{1.110}$ = 0.87, P = 0.35; species richness: $F_{1.110}$ = 1.1, P = 0.3; H’: $F_{1.110}$ = 0.2, P = 0.65), years (04/05 vs. 05/06) (abundance:

$F_{1.110}$ = 2.25, P = 0.14; species richness: $F_{1.110}$ = 0.06, P = 0.81; H’: $F_{1.110}$ = 1.15, P = 0.29) or regions (Northern areas vs. central areas vs. southern areas) (abundance: $F_{2.65}$ = 2.22, P = 0.38; species richness: $F_{2.65}$ = 2.48, P = 0.63; H’: $F_{2.65}$ = 1,52, P = 0.87). Therefore, we can state that our study is not affected by short term climatic conditions, time or area. For further analysis we pooled all data per vegetation scenario.

Vegetation state 1 and 2 (“non-degraded habitats”) displayed a higher abundance of reptiles and higher species richness than areas of vegetation state 3, 4 and 5 (“degraded habitats”). The vegetation scenario had significant effects on reptile abundance ($F_{4.51}$ = 58.36, $P < 0.001$), reptile diversity ($F_{4.51}$ = 48.48, $P < 0.001$) and species richness ($F_{4.51}$ = 44.57 $P < 0.001$). The Tukey-Tests showed that non-degraded habitats were significantly different from degraded habitats for abundance and species richness of reptiles (Figure 2 and 3).

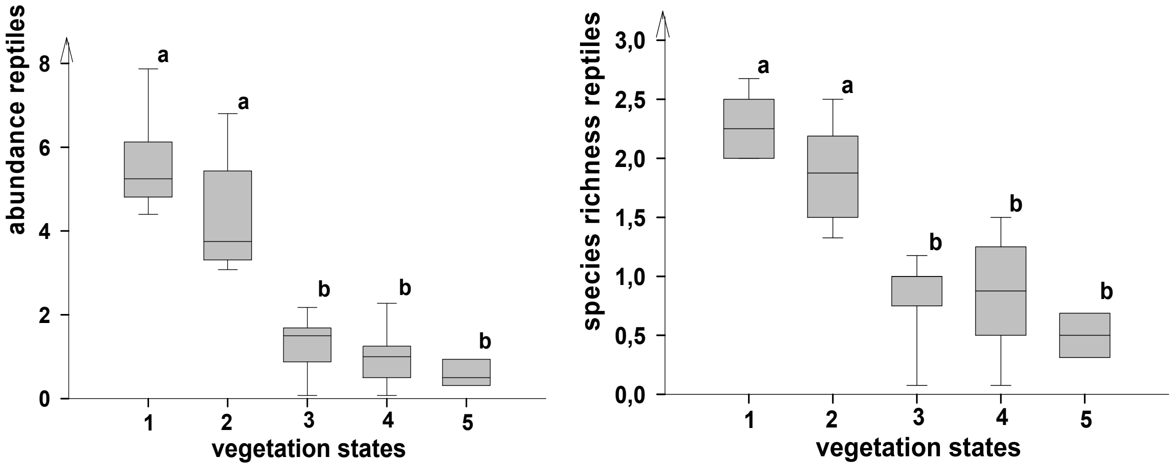

Figure 2-3 Means ± SE of abundance (no. of individuals) of reptiles and species richness (no. of species) of reptiles for the five vegetation states. Different letters (a, b) indicate significant differences between the respective vegetation scenario (ANOVA, Tukey Post Hoc Test, p-value < 0.05).

The analysis of the three dominant species (*Pedioplanis l. lineoocellata*, *Heliobolus lugubris* and *Mabuya variegata*) showed the same results. Abundance of *P. lineoocellata* and *M. variegata* was significantly lower on “degraded habitats” than on “non-degraded habitats” (Figure 4 and 5). Only *H. lugubris* displayed a partially different result: abundance in habitats of vegetation state 1 was significant higher than in “degraded habitats”, but vegetation state 2 displayed no significant difference (Figure 6).

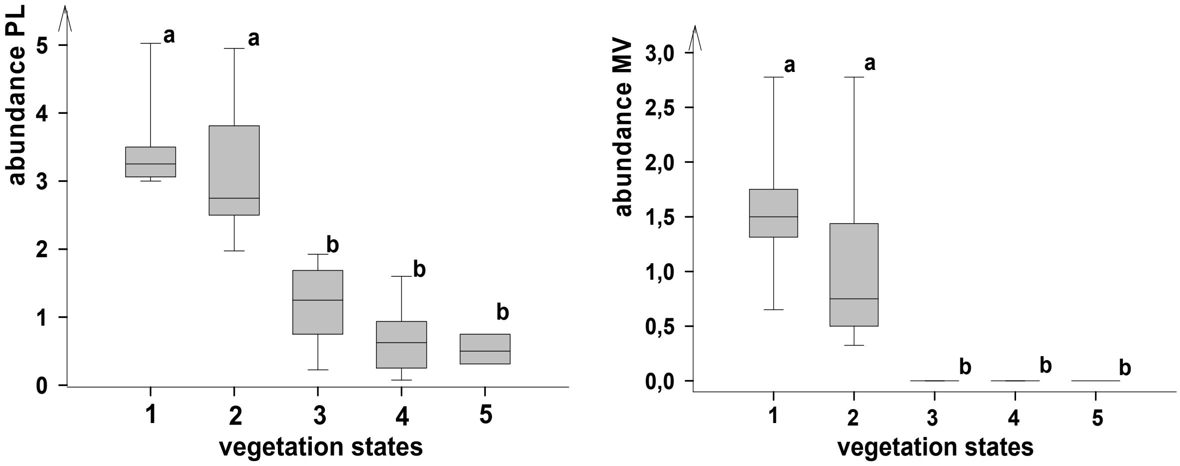

Figure 4-5 Means ± SE of abundance (no. of individuals) of *P. lineoocellata* (PL) and *M. variegata* (MV) of the five vegetation states. Different letters (a, b) indicate significant differences between the respective vegetation states (ANOVA, Tukey Post Hoc Test, p-value < 0.05).

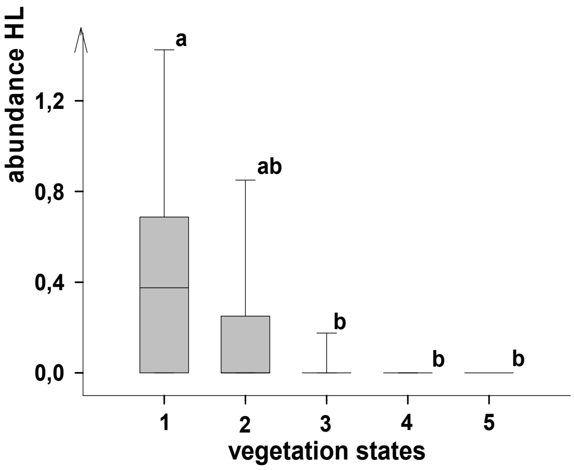

Figure 6 Means ± SE of abundance (no. of individuals) of H. lugubris (HL) of the five vegetation states. Different letters (a, b) indicate significant differences between the respective vegetation states (ANOVA, Tukey Post Hoc Test, p-value < 0.05).

4.3 Prey Availability

Orthoptera abundance was significantly lower on degraded habitats ($F_{4.51}$ = 325.19, P < 0.001). The Tukey-Test showed that the vegetation state 1 and 2 were significantly different from vegetation state 3, 4 and 5 for Orthoptera abundance (Figure 7).

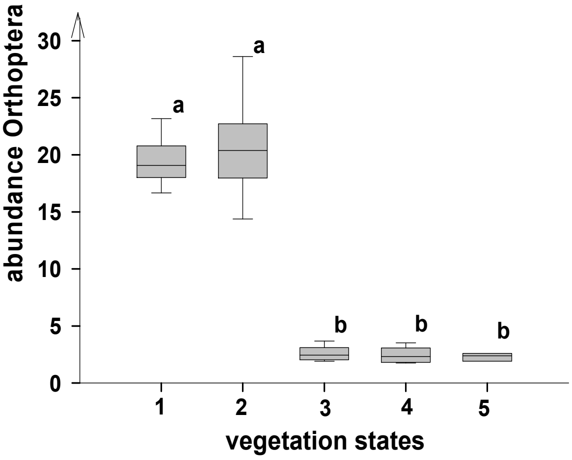

Figure 7 Means ± SE of abundance (no. of individuals) of Orthoptera for the five vegetation states. Different letters (a, b) indicate significant differences between the respective vegetation states (ANOVA, Tukey Post Hoc Test, p-value < 0.05).

4.4 Habitat Preference

An overview of habitat preference is given in table 3.

Table 3 Overview of the habitat (vegetation states) preference or avoidance of the three species (*P. lineoocellata* (PL), *H. lugubris* (HL) und *M. variegata* (MV))

Vegetation state	*P. lineoocellata*	*H. lugubris*	*M. variegata*
vegetation state 1	+	+	+
vegetation state 2	0	0	0
vegetation state 3	0	0	X
vegetation state 4	0	X	X
vegetation state 5	-	X	X

+: preference
-: avoidance
0: no preference
X: habitat not used

The G-Test (Table 4) for abundance of (i) *P. l. lineoocellata*, (ii) *H. lugubris* and (iii) *M. variegata punctulata* show that there was a highly significant difference between distributions of available and used vegetation states in the research area ((i) Chi ^{2} = 154.46, p < 0.001; (ii) Chi ^{2} = 71.37, p < 0.001**;** Chi ^{2} = 18.16, p = 0.0013) Hence, we rejected the null hypothesis that the three reptiles species use all vegetation states equally.

Manly's standardized selection index (B_i) showed that the three species preferred the vegetation state 1 ((i) B_i = 0.565; (ii) B_i = 0.824; (iii) B_i = 0.869). 56.5% of the individuals of P. lineoocellata, 82.4% of *M. variegata* and 86.9% of *H. lugubris* were found in vegetation state 1. Confidence limits of w_i indicate that these preferences are significant (Table 4). Vegetation state 5 was significantly avoided by *P. lineoocellata* (B_i = 0.022) and the two other species did not use this habitat at all. Additionally, the Variegated Skink did not occur in vegetation state 3, 4 and 5 as well as the Bushveld Lizard in vegetation state 3 and 5. All three lizard species show neither a preference nor an avoidance of the vegetation state 2. Furthermore, *P. lineoocellata* shows neither a preference nor an avoidance of vegetation state 3 and 4 as well as *H. lugubris* for vegetation state 4.

Table 4 Habitat preferences (selection indices) of the species: *Pedioplanis l. lineoocellata* (PL), *Heliobolus lugubris* (HL) und *Mabuya variegata* (MV)

Vegetation State	Proportion of vegetation state availability (p_i)	Prop. of reptiles in vegetation state (o_i)			Selection Index (w_i)			95% Confidence limit [a] of w_i						Standardized selection index[b] (B_i)		
		PL	HL	MV	PL	HL	MV	lower	upper	lower	upper	lower	upper	PL	HL	MV
								PL		HL		MV				
state 1	0.105	0.39	0.7	0.59	3.73*	6.64*	5.62*	2.58	4.89	2.55	10.73	3.51	7.73	0.57	0.87	0.82
state 2	0.339	0.35	0.27	0.41	1.038	0.79	1.2	0.69	1.39	0	2.02	0.55	1.86	0.16	0.10	0.18
state 3	0.31	0.05	0	0	0.14	0	0	0.33	1.44	0	0	0	0	0.02	0	0
state 4	0.153	0.14	0.03	0	0.89	0.22	0	0.1	1.52	0	1.32	0	0	0.13	1.32	0
state 5	0.093	0.08	0	0	0.81*	0	0	0	0.31	0	0	0	0	0.12	0	0

[a] Confidence limits with Bonferroni correction (α corrected = α/ n classes); α corrected to 0.01

[b] Standardized selection indices > 0.2 (1/ no. Of classes) indicate preference

* significant ($P < 0.05$)

5. Discussion

Our results clearly show that habitat degradation has strong negative effects on reptile communities in the southern Kalahari. This negative trend was found across study sites at a regional scale (~10000km^2). In degraded areas (vegetation state 4-5), which are characterized by high shrub cover and low perennial grass cover both abundance and species richness of reptiles was low. In contrast, in non-degraded habitats (vegetation state 1-2) where shrub cover was low and perennial grass cover high, abundance and species richness of reptiles were high (state 1). A partial loss of perennial grass cover (state 2) had little to no effects on local species abundance and richness. Nevertheless, the habitat preference analysis of single species showed that the three most common reptile species (*P. lineoocellata*, *H. lugubris* and *M. variegate*) preferred non-degraded habitats over areas where grazing reduced perennial grass cover (degraded habitats).

Degraded habitats are characterized by loss of perennial grasses and herbaceous vegetation (Van Vuren and Coblentz 1987, Fleischner, 1994) and a decline of vegetation diversity (Blaum et al. 2007). As the structures of *Rhigozum trichotomum*, the dominating shrub species in degraded habitats, and of the annual grass *Schmidtia kalaharensis*, the dominant grass species under these conditions, are not as dense as the tussocks of perennial grasses like e.g. *Stipagrostis ciliata* or *Centropodia glauca* similar effects as after vegetation loss occur under shrub encroached conditions: First the possibility for reptiles to thermoregulate is retained and second the risk of predation is increased. Furthermore, a decrease of vegetation diversity and cover is followed by a principle decline of resource availability (prey abundance) (Figure 7) also shown by previous work on arthropod abundance by Gandar (1982), Dean and Milton (1995) and Seymour and Dean (1999). All three components (thermoregulation, predation risk and resources availability) can contribute to lower reptile abundance and species richness in degraded habitats on the regional scale.

5.1 Thermoregulation

The loss of vegetation cover reduces the availability of thermoregulatory patches and thus intensifies environmental extremities (severity) for reptiles (Saunders et al. 1991, Attum et al. 2006b, Wasiolka unpublished data). In degraded habitats the ratio of sunny spots (to heat up) and shaded spots (to cool down) is shifted to the side of the sunny spots. Decreasing number of shady patches and decreasing patch size increases the distances and time across which reptiles have to travel to reach the next suitable patch for thermoregulation. This can possibly lead to an increase of predation risk due to longer distances travelled (see predation risk) and/or to a decrease in foraging efficiency (Chapter 2).

5.2 Predation risk

For many species vegetation serves as a retreat or safe site (Norbury 2001, Wasiolka 2004). Loss of vegetation and resulting open areas are often associated with increased predation risk (Brown et al. 1988, Kotler et al. 1991, Bentley et al. 2000, Norbury 2001). Due to the loss of cover reptiles are more conspicuous to possible predators like raptors or small carnivores and stand a higher chance to fall victim to them. Furthermore, reptiles move longer and further in degraded habitats in the search of prey (McLoughlin and Ferguson 2000) and therefore are even more susceptible to predation (MacArthur and Pianka 1966).

5.3 Resource availability

Both, high abundance and high species richness is supported by the higher prey availability in non-degraded savannah habitats (Dean and Milton 1995, Seymour and Dean 1999). As a consequence of lower grass cover in degraded habitats abundance of grasshoppers that feed on grassy vegetation (Hutchinson & King 1980) declines. Also in this study prey availability in non-degraded habitats was significantly higher for insectivorous lizards (all species) (see also Pianka 1986, Branch 1998). The same is valid for all of the encountered snake species which mainly feed on lizards and/or other snakes (Branch 1998, Marais 2004) and therefore would benefit from higher reptile abundance in non-degraded habitats. A possible adaptation to limited food resources in degraded habitats could be to enlarge home range size to compensate for lower prey availability (Wauters and Dhondt 1992).

5.4 Habitat preference

We showed that the reptile diversity decline with increasing degradation state does not only hold for the reptile community as a whole but also for single lizard species (*P. lineoocellata*, *H. lugubris* and *M. variegata*). The importance of perennial grass cover is supported by the documented preferences of reptiles for habitats with high perennial grass cover and vegetation diversity. Huey and Pianka (1977) already showed for the southern Kalahari that *Mabuya variegata* is associated with bunch grasses and hence more abundant on sites with higher perennial grass cover, the non-degraded habitats. Clearly, the response of species to habitat degradation depends on their specific needs and adaptation capabilities. It is likely that the survival of an abundant and widely distributed species such as *P. lineoocellata* would be not as much affected by degradation as rarer species with a smaller distribution area. On the other hand species that are adapted to disturbances might even benefit from overgrazing (see Ballinger and Jones 1985).

5.5 Conclusion

Reptile abundance and diversity decline with habitat quality. This is probably because their ability to thermoregulate, reduce predation risk and obtain food are negatively influenced by grazing induced habitat changes in the southern Kalahari. Thus, to maintain high regional reptile diversity in this savannah it will be of importance to preserve non-degraded habitats with maximum habitat quality. A vital factor affecting this quality is amount of perennial grass cover, which turned out to be one of the driving forces behind reptile species diversity under the harsh conditions of the semi arid southern Kalahari. To ensure such a high level of perennial grass cover it is necessary to protect non-degraded habitats from overgrazing at the landscape (regional) scale. In contrast to common species like the lizard *P. lineoocellata* which can compensate loss of suitable habitat by having high numbers individuals, large, fairly undisturbed areas are particularly important for rarer species such as *Mabuya occidentalis*.

To quantify the influence of thermoregulation, predation risk and resource availability on reptile diversity and abundance and to gain a deeper insight into the relationship between reptile diversity and the effects of overgrazing on the vegetation structure and composition we suggest implementing controlled experimental manipulation like food supplementation, removal/adding of perennial grasses or relocation experiments.

For both, conservation and rangeland management overgrazing and resulting shrub encroachment are of major concern, as the latter reduces livestock carrying capacity and reduces regional species diversity. Both sides would benefit if they work hand in hand to solve the problems caused by commercial farming to ensure having high species diversity in the long term and sustainable land use.

6. References

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Link to chapter two

In chapter one I investigated the impact of grazing-induced savannah degradation on the reptile communities in the southern Kalahari. My results are a first assessment of diversity and abundance patterns of reptiles under land use in Kalahari rangeland. To obtain a deeper understanding of the role of human mediated habitat degradation on different aspects of the life history of reptiles the proceeding chapters focus on the most abundant species, the Spotted Sand Lizard (*Pedioplanis lineoocellata lineoocellata*).

P. lineoocellata belongs to the family lacertidae. Its coloration ranges from buff to grey-brown or red-brown, usually with two to four rows of dorsolateral pale spots. Four to seven prominent bluish-whitish spots are present at the flanks. The tail is flecked and the belly whitish. Snout-vent length ranges from 46.8 to 63.8mm and tail length from 92.1 to 155.3mm with a body mass up to 7.3g (own measurements). In the southern Kalahari the lizard prefers sandy areas (own observations). It is a sit-and-wait hunter and its diet consists of a variety of arthropods depending on season (Branch 1998). During November females lays up to eight eggs and hatchlings leave eggs after 70-80 days (Branch 1998).

In chapter two I investigate behavioural responses of *P. lineoocellata* to habitat degradation. In particular, I analyse behavioural adaptations in activity and movement patterns as response to changing habitats. Behavioural responses can help to understand changes in distribution and abundance of species as well as shifts in population dynamics.

Branch B. (1998) Field guide to snakes and other reptiles of Southern Africa. Struik Publisher, South Africa

Chapter 2

Impact of overgrazing: Behavioral responses of the lizard *Pedioplanis l. lineoocellata*

Pedioplanis l. lineoocellata (juvenile)

Impact of overgrazing: Behavioral responses of the lizard *Pedioplanis l. lineoocellata*[1]

1. Abstract

We studied the foraging behaviour of the lizard *Pedioplanis l. lineoocellata* (Spotted Sand Lizard), a sit and wait forager, in habitats of different vegetation states to determine the effects of habitat degradation on this species. At high grazing intensity where vegetation cover and diversity is low, the lizard *P. lineoocellata* moves more frequently, spends more time moving and covers larger distances than in habitats where vegetation cover and diversity is high. These behavioural changes in movement patterns can be explained by less abundant prey in habitats with low vegetation cover and diversity. Although morphology and physiology of *P. lineoocellata* should constrain the change in foraging behaviour the species has modified its foraging strategy from sit and wait to actively foraging. We assume that this behavioural flexibility of *P. lineoocellata* is a buffer mechanism enabling the species to use and survive in degraded (unfavourable) habitats.

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[1] This chapter is submitted as:
Wasiolka B., Henschel J. and Jeltsch, F.: Impact of overgrazing: Behavioral responses of the lizard *Pedioplanis l. lineoocellata*. Acta Oecologica

2. Introduction

For decades human land use practices including livestock grazing, game ranching, fire suppression or firewood cutting in semiarid savannahs of southern Africa have altered the vegetation composition and structure of the system (e.g. Leistner, 1967; Hanley and Page 1982; Skarpe, 1991b; Jeltsch et al., 1996; Dean et al., 1999; Meik et al., 2002). High grazing pressure by herbivores, especially by domestic livestock (Prins and van der Jeugd, 1993; Jeltsch et al., 1997; Roques et al., 2001) usually causes overgrazing. Overgrazing leads to a reduction of perennial grass cover and herbaceous vegetation cover (Skarpe, 1990b; Wiegand et al., 2005) resulting in increased availability of bare soil (Skarpe, 1990a). Increase of bare soil and decrease of competition by perennial grasses favours shrub establishment on open ground (Skarpe, 1990b; Teague and Smit, 1992; Jeltsch et al., 1997). In the long term these dynamics lead to relatively uniform and homogenous shrub thickets (Jeltsch et al., 1996; Dean et al., 1999; Roques et al., 2001), a phenomenon referred to as shrub encroachment.

The resulting changes in vegetation composition and cover alter environmental conditions for a variety of species such as lizards in a way that habitat quality decreases. For lizards it has been shown that the above mentioned effects of overgrazing lead to a decline of lizard diversity and abundance (Busack and Bury, 1974; Reynolds, 1979; Ballinger and Watts, 1995; Brown et al., 1997; Meik et al., 2002). Furthermore, reduction of perennial grass cover affects invertebrate diversity and abundance negatively as well (Gandar, 1982; Dean and Milton, 1995; Dennis et al., 1998; Seymour and Dean, 1999). This is an important factor because invertebrates represent the main prey source of many lizard species in the Kalahari (Pianka, 1986).

The main focus of recent investigation emphasized the impact of overgrazing and shrub encroachment on lizard community structure, distribution, abundance and prey density (Huey and Pianka, 1977; Jones, 1981; Bock et al., 1990; Brown et al., 1997; Meik et al., 2002; Wasiolka, 2004). But also it is important to investigate behavioural responses of species to habitat alteration to gain more information about population dynamics on natural and degraded habitat. Behavioural responses can help to understand changes in distribution and abundance of species as well as shifts in population dynamics. Furthermore, behavioural adaptations can possibly buffer the disadvantages of degraded habitats. Yet very few studies have examined the impacts of habitat degradation on behaviour ecology of lizards. Hence, our study is one of the first that deals with behavioural responses of a lizard species to overgrazing.

We chose the lizard species *Pedioplanis l. lineoocellata* (Spotted sand lizard) as our study object as it is a fairly abundant, widely distributed, and utilizes a variety of different habitats. Therefore, it is an ideal species to investigate if lizard species show different behaviour responses to natural and degraded habitats. This species is a sit-and-wait predator (Huey and Pianka, 1981).

We conducted standardized observations of lizards and their prey in habitats with different vegetation states and thus with different vegetation structure and diversity. We addressed the following hypotheses: (1) Prey abundance decreases with increasing degradation of habitat; (2) As a consequence *P. lineoocellata* moves more frequently, spends more time moving and covers larger distances in the in the search of less abundant prey in degraded habitats.

3. Methods

3.1 Study Area and Period

The study was conducted from November 2004 to February 2005 on six privately owned farms (Vry Soutpan (S 27°17’04.0”; E20°50’19.7”), Swartpan (27°15’36.3”; E20°46’18.4”), Loch Lemond (S 27°03’40.7”; E 020°45’28.7”); Rea (S 27°01’07.7”,E 20°40’06.6”) Rooiduin (S 26°42’46.3”, E20°35’10.3”) and Hoekrans (S 26°39’22.0”, E 20°34’55.5”)) around Askham, Northern Cape in the vicinity of the Kgalagadi Transfrontier Park in the southern Kalahari, South Africa. The region is classified as an arid savannah (van Rooyen, 2001) with an annual rainfall of 150mm to 300mm (Leistner and Werger, 1973) which falls mainly in summer (Werger, 1978). Temperature extremes range from winter lows reaching –10.3 °C to summer highs up to 45.4 °C (van Rooyen, 2001). The vegetation type is classified as the western form of the Kalahari Thornveld (Acocks, 1988). The typical form is an extremely open savannah with scattered trees of *Acacia erioloba* and *A. haematoxylon*. Other important woody vegetation species are the tree *Boscia albitrunca* and the shrubs

Grewia flava, Lycium hirsutum, Acacia mellifera and *Rhigozum trichotomum*. The main grass species are *Aristida* ssp. and *Eragrostis* ssp. in the valleys and *Centropodia glauca, Stipagrostis namaquensis, Stipagrostis uniplumis, Monechma incanum* and *Crotalaria virgultalis* on dunes (Leistner, 1959; Pianka and Huey, 1971; Acocks, 1988).

3.2 Vegetation Survey

We chose five different vegetation states which are characterized by different (Table 1) vegetation composition, cover, structure and diversity. These five vegetation states were chosen because they represent vegetation states generated by low –and high grazing pressure as well as by short –and long term effects. Vegetation state 1 (low grazing pressure/short term effect) and vegetation state 5 (high grazing pressure/long term effect) are two states at opposite ends of the spectrum (Walker et al., 1981; Skarpe, 1990; Moleele and Perkins, 1998). The three other vegetation states are intermediate states (Walker et al., 1981).

Table 1 Range of vegetation cover of shrubs, perennial grasses, annual grasses, herbs and bare ground and plant diversity (Shannon Index) for the five vegetation states

Vegetation state	Vegetation cover (%)					Vegetation diversity (Shannon Index)
	shrubs	perennial grass	annual grass	herbs	bare ground	
vegetation state 1	0	31-38	0-1	2-6	57-61	0.72
vegetation state 2	0-1	19-30	5-8	1-6	57-71	0.78
vegetation state 3	13-19	3-7	8-12	0-2	65-72	0.51
vegetation state 4	27-34	1-2	2-10	0-1	60-66	0.31
vegetation state 5	0-1	0-2	19-32	0-1	75-80	0.22

To quantify the differences in vegetation composition, cover and diversity, we sampled two parallel transects 250m long and 20m-30m apart in each of the sampled sites of the observation study. Starting after 25m on each transect every 50m a 5 by 5m square was surveyed. Percent ground cover of shrubs, perennial grasses, annual grasses, herbaceous vegetation and bare ground was estimated and the mean calculated. In addition, we calculated the Shannon Index (e.g. Shannon, 1948) to estimate plant diversity. In total we sampled 50 vegetation transects.

3.3 Behavioural Observations

Focal observations took place in dune valleys at sites that differed in vegetation composition, structure and diversity (Table 1). To exclude effects on lizard behaviour by different vegetation composition than the actual study site, each study site was part of a much larger area consisting of similar vegetation composition. The dune valleys were observations took place were at least 80m wide and 500m long. Furthermore, the neighbouring dune valleys consisted of similar vegetation composition.

During the study period adult individuals of the lizard *Pedioplanis l. lineoocellata* were observed directly using 8-fold magnifying binoculars. Focal-animal observations were conducted during the morning (8.00 a.m. to 10.00 a.m.) and afternoon (4.00 p.m. to 6.00 p.m.) (Nagy et al., 1984). Lizard observations were equally distributed within these times. During inclement weather conditions (i.e. windy and/or rainy days) no lizard observations took place. Whenever an undisturbed individual of *P. lineoocellata* was encountered it was observed from a distance between 5m to 8m. Individuals of *P. lineoocellata* were observed continuously for 15 min. if possible. To compensate for disturbance of lizards by the observer’s presence, the first minute of each observation was omitted from further analyses. Observation time totalled 25.3 hr, during which 104 focal observations were performed, ranging from 8.8 min to 14 min in duration. The time each individual spent being active and passive were recorded. In addition, the approximate distance each individual covered while moving was noted. Distances (in meter) of movements were estimated visually by the same observer. Care was taken to sample each individual only once by walking along the respective dune valley without returning to the same area again.

We observed and measured the following parameters: (i) moves per minute (MPM), ii) percentage time spent moving (PTM) and (iii) total distance (TD) covered by each individual.

3.4 Prey Abundance

Orthoptera smaller than 2.5 cm in body length are one of the main food sources of *P. lineoocellata* (pers. obs.), especially during summer (Pianka, 1986), the investigation period. We surveyed Orthoptera (grasshoppers, locusts) abundance in the same habitats as the focal observations of *P. lineoocellata.* This was done with Visual Encounter Surveys along 100m transects. We counted all Orthoptera smaller than 2.5cm in a 1.5m wide corridor to both sides of the transects. A total of 64 transects were surveyed.

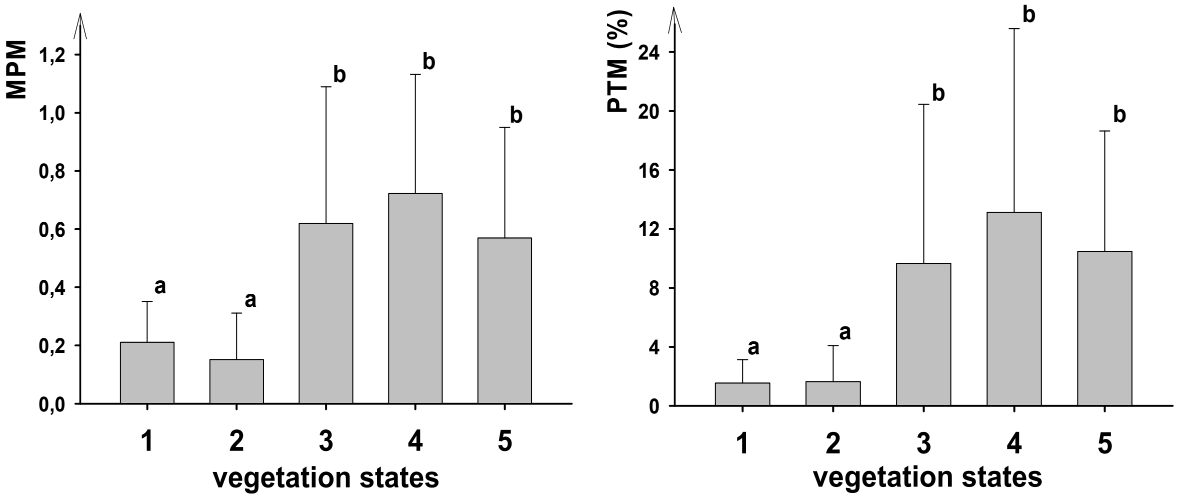
3.5 Data Analyses

We calculated moves per minute (MPM) and the percentage time spent moving (PTM) to identify foraging mode (Huey and Pianka, 1981; Perry, 1999). For calculations of PTM all behaviour patterns considered as active (e.g. moving and hunting) were combined. To calculate total distance (TD) all distances that an individual moved were added. For observations shorter than 14min. TD was corrected to 14minutes. To evaluate MPM, PTM, TD and Orthoptera abundance the means were compared.

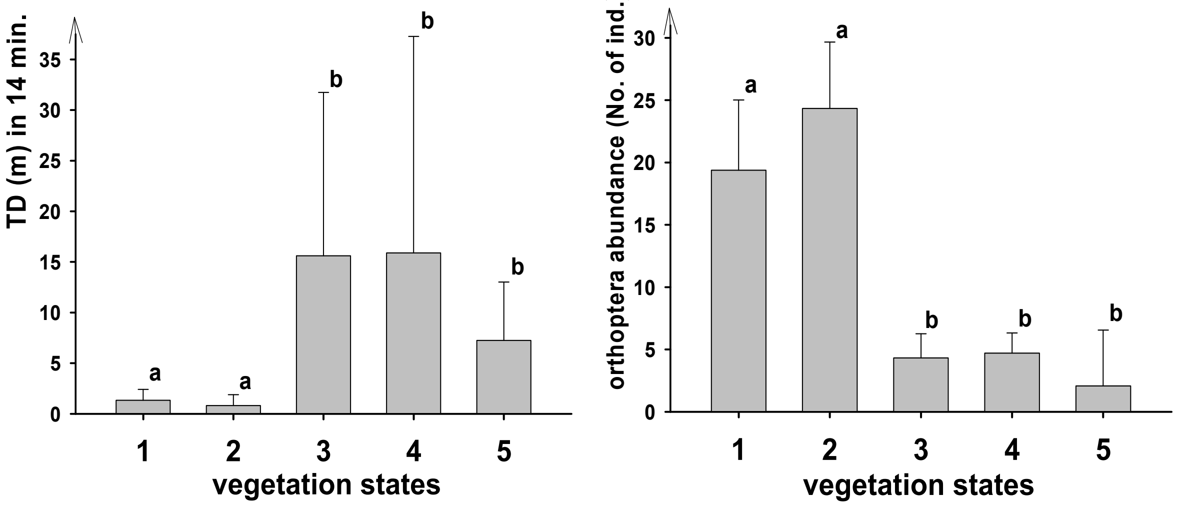
Data were analyzed by means of the statistical program SPSS, Version 12.0 (© SPSS Inc.). To meet the assumptions of parametric tests, normal distribution and homogeneity of the data, all data sets were LN(x+0.1)-transformed (Underwood, 1997). MPM, PTM, linear distance, total distance and Orthoptera abundance data were analyzed using one-factor ANOVA (Dytham, 1999). In addition, Post-Hoc-Tests (Tukey-Test) were applied to test for significant differences between the vegetation states. For all tests P-value of < 0.05 was regarded as statistically significant.

4. Results

Individuals of *P. lineoocellata* at vegetation state 3,4 and 5 (“degraded habitats”) displayed a higher movement rate (MPM), a longer activity time (PTM) than the individuals did in vegetation state 1 and 2 (“natural habitats”) (Figure 1 and 2). Furthermore, the individuals travelled longer distances (TD) on degraded habitats (Figure 3). Furthermore, Orthoptera abundance was lower on degraded habitats (Figure 4). The vegetation state had significant effects on moves per minute ($F_{4.99}$ = 12.55, $P < 0.001$), percentage time moving ($F_{4.99}$ = 15.20, $P < 0.001$), total distance ($F_{4.99}$ = 18.78, $P < 0.001$) and Orthoptera abundance ($F_{4.59}$ = 21.196, $P < 0.001$). The Tukey-Tests showed that the vegetation state 1 and 2 were significantly different from vegetation state 3,4 and 5 for MPM, PTM, TD and Orthoptera abundance (Figure 1 to 4). As a consequence P. lineoocellata moved more frequently, spent more time moving and covered larger distances in the search of less abundant prey.



Figures 1-2 means ± SE of moves per minute (MPM), percentage time moving (PTM) for the five vegetation states. Different letters (a, b) indicate significant differences between the respective vegetation states (ANOVA, Tukey Post Hoc Test, p-value < 0.05). The graphs show the original data.



Figures 3-4 means ± SE total distance (TD) and Orthoptera abundance for the five vegetation states. Different letters (a, b) indicate significant differences between the respective vegetation states (ANOVA, Tukey Post Hoc Test, p-value < 0.05). The graphs show the original data.

5. Discussion

We investigated the impact of overgrazing on the behaviour ecology of *Pedioplanis l. lineoocellata*. We sampled moves per minute (MPM), percentage time moving (PTM), total distance (TD) and Orthoptera abundance to obtain information on behavioural responses to habitat degradation and the resulting consequences for the species.

The results of moves per minutes (MPM) and percentage time spent moving (PTM) showed that the lizard species *P. lineoocellata* moved more frequently and spent more time moving in degraded (vegetation state 3,4 and 5) in comparison to natural habitats (vegetation state 1 and 2). Additionally, total distance (TD) demonstrated that *P. lineoocellata* covered larger distances in degraded habitats than in natural habitats. Furthermore, our results of prey abundance showed that Orthoptera abundance decrease with habitat degradation. These results support our hypotheses that *P. lineoocellata*: (1) in the search of less abundant prey (2) moves more frequently, spends more time moving and covers larger distances in degraded habitats.

The results of our study regarding MPM, PTM and TD point out that the sit and wait forager *P. lineoocellata* modifies its foraging strategy on degraded habitats that support less prey compared to natural habitats. The lizards no longer use a clear sit and wait strategy (specific for mobile prey) but their behaviour resembles an active foraging strategy (more specific for sedentary food). Perry (1999) considered PTM > 10% as the criterion for active foraging. Our results of PTM indicate that the three degraded habitats (9.66 - 13.13%) are higher or close to that level compared to a PTM of 1.54% and 1.64% in natural habitats. These findings are surprising because the type of foraging mode is linked to morphological traits such as body shape, body weight and relative clutch size (Anderson and Karasov, 1988; Wymann and Whiting, 2002) further influenced by physiology, predators and competitors (Eifler and Eifler, 1999). Active foragers are more slender, incur higher energy costs and have greater stamina (Cooper and Whiting, 2000; Butler, 2005) than sit and wait foragers. In addition the main defence strategy of an actively forager is speed compared to the sit and wait forager who rely on crypsis as primary defence (Vitt, 1983). However, it should be noted that values of PTM for *P. lineoocellata* were only slightly higher than the threshold of 10% and are far lower than PTM's of the distinctly active forager like *Mabuya striata sparsa* (PTM: 41.8%) or *Heliobolus lugubris* with a PTM of 57% (Huey and Piank, 1981; Wymann and Whiting, 2002). Likewise, MPM (0.57 - 0.72) are lower than typical figures of active foragers (Cooper and Whiting, 1999). However, again, they are 3 to 4 times higher than in less disturbed habitats and still higher than typical figures of sit and wait foragers (e.g. *M. spilogaster*: MPM = 0.31). The high values of TD in degraded habitats are typical for active forager because the cover larger distances as they search for prey (Wymann and Whiting, 2002)

Hence, this lizard species seems to be able to adapt to increasing habitat degradation by changing its foraging mode from a distinct sit and wait behaviour closer to an actively foraging mode. Although morphology and physiology of *P. lineoocellata* should constrain the change in foraging behaviour the species is able to adjust its foraging strategy to the availability and distribution of prey.

This behavioural shift coincides with a decrease in Orthoptera abundance on degraded habitats. A decrease of arthropod density on degraded habitats was also reported by Gandar (1982), Dean and Milton (1995) and Seymour and Dean (1999).

The chance to find patches with high prey densities or to encounter prey more frequently are higher while moving around than to wait for prey to pass by (Huey and Pianka, 1981; Cooper and Whiting, 2000; Greef and Whiting, 2000). Hence, our results on *P. lineoocellata* support Greef and Whiting (2000) who stated that lizards are adept at solving foraging problems, e.g. by shifting their foraging behaviour in response to changes in resource availability.

In the literature only few studies describe shifts in foraging behaviour in response to food availability in lizard species. The few existing studies identified seasonal and short term shifts (Pietruszka, 1986; Lister and Aguayo, 1992; Eifler and Eifler, 1999; Greef and Whiting, 2000) in response to fluctuations of food. Similarly, scorpions have been reported to change their foraging strategy during short periods of food stress (Polis, 1988). Habitat degradation leads to prolonged reduction of prey abundance, which would result in a long-term change of foraging strategy by *P. lineoocellata*. A short time adaptation is not sufficient in this case since on overgrazed habitats prey availability does not shift seasonally but is reduced permanently. Similar long term changes for a reptile species have been documented for the Tiger Snake (*Notechis ater occidentalis*). Aubret (2004) documents a shift in prey and hunting strategy for this species as a consequence of utilizing different habitats.

We assume that this behavioural flexibility of *P. lineoocellata* is a buffer mechanism enabling the species to use and survive in degraded (unfavourable) habitats. However, the risk of predation increases with the length of foraging activity (Polis, 1988). In addition, active foragers are more prone to encounter predators (Huey and Pianka, 1981; Munger et al., 1983; Wymann and Whiting, 2002; Attum and Eason, 2006). Thus, the increase in activity of *P. lineoocellata* and the decrease of cover can result in higher predation risk (Bentley et al., 2000; Norbury, 2001) - the chance to fall victim to a predator (e.g. snake, raptor) could be higher in degraded habitats.

If prey abundance for populations within the same species decrease, as a compensatory mechanism home range size often increases for reptiles (Wauters and Dhondt, 1992; Powell et al., 2000) as well as for other taxa (Hixon, 1980; Pejchar et al., 2005). A similar response can be expected for *P. lineoocellata*: home range size may increase.

As a consequence of less abundant prey in degraded habitats (vegetation state 3, 4 and 5) the carrying capacity of *P. lineoocellata* can be reduced in comparison to natural habitats (vegetation state 1 and 2). Therefore, we suggest testing, if the change in the lizards foraging strategy buffers the lower prey availability or if the abundance of *P. lineoocellata* declines as a consequence of overgrazing resulting in less abundant prey. Comparable studies on other reptile species should determine whether the observed behavioural changes and its consequences are a more general phenomenon under the impact of habitat degradation. *P. lineoocellata,* as an abundant and widely distributed species, is probably not as much affected by degradation as a rarer species with a smaller distribution area would be. The more important are studies that identify and evaluate possible (behavioural) mechanisms that are at least partially able to buffer against the possible negative effects of overgrazing and shrub encroachment. Furthermore, the identification of limits and thresholds of behavioural adaptations as well as the role of possible negative feedbacks (e.g. increased predation) could provide useful recommendations for conservation strategies and habitat management.

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Link to chapter three

In the second chapter I investigated behavioural adaptations in activity and movement patterns of *Pedioplanis l. lineoocellata* to habitat degradation. The results showed that the lizard moves more frequently, spends more time moving and covers larger distances in degraded than in non-degraded habitats. These results suggest that *P. lineoocellata* not only increase its search activity in degraded habitats but also increase home range size. To test this assumption I radio tracked *P. lineoocellata* and analysed in chapter 3 the living space of the lizard one of the most important resources an animal uses.

Chapter 3

Space use of the Spotted Sand Lizard (Pedioplanis l. lineoocellata) under different degradation states

Space use of the Spotted Sand Lizard (Pedioplanis l. lineoocellata) under different degradation states [1]

1. Abstract

Although the effects of grazing induced savannah degradation on animal diversity are well documented, knowledge of how they affect space use or responding behavioural adaptations remains poor. In this study, we analysed space use of the Spotted Sand Lizard (*Pedioplanis l. lineoocellata*) in degraded versus non-degraded habitats southern Kalahari savannah habitats. Lizards were radio tracked, daily movement distances recorded and home range sizes calculated. In degraded Kalahari savannah habitats where plant diversity and perennial grass cover are low but shrub cover high, *P. lineoocellata* moves larger distances (40.88 ±6.42m vs. 27.43 ±5.08m) and occupies larger home ranges (646.64 ±244.84m^2 vs. 209.15 ±109.84 m^2) than in non-degraded habitats (high plant diversity, high perennial grass cover and low shrub cover). We assume that this increase in daily movement distances and home range sizes is a behavioural adaptation to limited food resources in degraded savannah habitats. Although *P. lineoocellata* is able to adapt to resource poor savannah habitats, the increase in the lizard’s movement activities is likely to result in a higher predation risk. This is supported by the lower availability of protective vegetation i.e. perennial grass cover. Hence, we conclude that despite behavioural flexibility of *P. lineoocellata* overgrazing has a severe negative impact on the space use of *P. lineoocellata*.

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[1] This chapter is submitted as:
Wasiolka B., Jeltsch F., Henschel J., and Blaum N.: Space use of the Spotted Sand Lizard (Pedioplanis l. lineoocellata) under different degradation states. Animal Conservation

2. Introduction

World wide anthropogenic land use e.g. livestock grazing, game ranching and firewood cutting has altered vegetation composition and structural diversity of savannah ecosystems (e.g. Archer et al. 1988, Jeltsch et al. 1996, Roques et al. 2001, Sankaran et al. 2005). One of the most threatening forms of savannah degradation is heavy grazing induced shrub encroachment at the cost of perennial grasses and herbaceous vegetation (Skarpe 1990, Teague and Smit 1992, Jeltsch et al. 1997, Van Auken 2000 and Wiegand et al. 2005). In particular, shrub encroachment has become increasingly evident over the past five decades in the savannah of southern Kalahari (Leistner 1967, Skarpe 1991, Tews et al. 2004). Area wide shrub encroachment has led to habitat fragmentation of savannah rangelands and reduced abundance and diversity across animal taxa (arthropods: e.g. Dennis et al. 1998 and Seymour and Dean 1999; birds: e.g. Thiele et al in press; mammalian carnivores: Blaum et al. 2007a, Blaum et al. in press; reptiles: Meik et al., 2002, Wasiolka 2004; rodents: Blaum et al. 2007b, Blaum & Wichmann in press).

Although the impacts of habitat degradation on animal diversity across taxa are well documented, knowledge of the possible impact of savannah degradation on species life history e.g. space requirements or behavioural adaptations remains poor. Particularly living space (generally described as “home range”) in changing environments is one crucial factor affecting species occurrence and is one of the most important resources an animal uses. It is defined as the area an animal utilized during it daily activities of e.g. feeding and breeding (Burt, 1943). Home rage is characterized typically with descriptors of its size, shape and structure (Kenward 2001). In our study we concentrated on home range size which is the most commonly used animal space use estimators in ecological research. Important factors that can affect home range sizes in reptiles include season, sex, body size, population size, foraging behaviour and social behaviour. The influence of these factors is well documented in the literature (e.g. Rose 1982, Al-Johany and Spellerberg, 1989, Zuffi et al. 1999, Guarino 2002). While the majority of home range size studies focused exclusively on one habitat type for a variety of species (e.g. Slip and Shine 1988, Smith 1995, Knapp and Owens 2005, Kerr and Bull 2006), but only few studies analysed changes in home range size in relation to different levels of habitat degradation.

In particular knowledge of possible adaptations of lizard's home range size in response to changing habitats is lacking. Previous studies in degraded savannah habitats where vegetation cover and diversity are low demonstrated that the lizard *Pedioplanis l. lineoocellata* increases its daily movement activity, i.e. distance moved and time moving, than in non-degraded habitats where vegetation cover and diversity are high) (see Chapter 2). These results suggest that *P. lineoocellata* increases its search activity in degraded habitats but also increase home range size.

To test this hypothesis we radio tracked study *P. lineoocellata*, a medium sized, diurnal, ground dwelling lizard (Branch 1998) in two Kalahari savannah habitats which differ largely in their level of habitat degradation (i.e. vegetation composition and structural diversity). Non-degraded habitats are characterized by low shrub cover, high perennial grass cover and high plant diversity whereas in degraded habitats shrub cover was high and perennial grass cover and plant diversity low.

The following hypotheses are addressed: (1) In non-degraded habitats home range size of *P. lineoocellata* is smaller than in degraded habitats. (2) In degraded habitats lizards select microhabitats of higher structural diversity more frequently than of lower structural diversity relative to microhabitat availability within its home range. In non-degraded habitats *P. lineoocellata* does not show any preference.

3. Methods

3.1 Study area

We investigated the home range size of the Spotted Sand Lizard, *Pedioplanis l. lineoocellata* in the savannah rangeland of the southern Kalahari, South Africa. The survey was conducted on the farm "Loch Lemond" (S 27°02'; E 20°44') approximately 70 km south of Twee Rivieren, Kgalagadi Transfrontier Park, South Africa.

The savannah vegetation is described as the Auob dune veld characterized by a continuous grass layer (e.g. *Centropodia glauca, Stipagrostis uniplumis, S. ciliata*) and a discontinuous woody layer of trees (e.g. *Acacia erioloba, A. haematoxylon* and *Boscia albitrunca*) and shrubs (e.g. *Lycium hirsutum, Acacia mellifera* and *Rhigozum trichotomum*) (Mucina et al. 2005). The region is classified as an arid savannah with an annual rainfall of 150mm to 300mm which falls mainly in summer (van Rooyen, 2001).

3.2 Habitat selection

We selected two habitats of different degradation state. Non-degraded habitats are characterized by high perennial grass cover, low annual grass cover, low shrub cover and high plant diversity. Degraded habitats show low perennial grass cover, high annual grass cover, high shrub cover and low plant diversity (Table 1).

Table 1 Proportion of bare ground, vegetation cover of shrubs, perennial grasses, annual grasses, herbs, and diversity index (H') in two savannah habitats (non-degraded vs. degraded).

Habitat type	Vegetation cover (%)					
	Shrubs	Perennial grass	Annual grass	Herbs	Bare ground	Diversity Index (H')
non-degraded	0-1	31-38	0-1	2-5	57-65	0.72
Degraded	13-18	3-9	7-12	0-2	65-76	0.51

3.3 Radio tracking

Animals were radio tracked during October 2005, the dry season and February the following rainy season. Lizards were captured with the aid of a fishing rod fitted out with a noose (Guarino, 2002) and checked for sex.

Earlier radio tracking studies have shown that home range size differ between sexes (e.g. Smith 1995, Jurczyszyn and Zgrabczynska 2007) we selected only male animals to gain a larger set of comparable data. All females were released immediately and males were measured and weighed. Only males those were heavy enough (< 7.5% of the animals weight (Kenward 2001) were fitted with transmitters (weighing 0.36g) (Table 2). The transmitters were glued to the backs of the males (149 MHz transmitters; type LB-2N, manufactured by Holohil Systems Ltd., Canada).

The radio tracking setup was approved by the Northern Cape Nature Conservation Service (Permit No. 0953/04 & 0014/06). The transmitters did not appear to have any detrimental effects on the lizards (B. Wasiolka unpublished data).

Table 2 Characteristics of study animals in two savannah habitats (non-degraded vs. degraded) separated in dry and wet season. Snout-vent length (SVL), tail length (TL), body mass and no. of bearings of *P. lineoocellata* fitted out with transmitters.

Habitat type	Season	Lizard no.	SVL (mm)	TL (mm)	Mass (g)	No. of bearings
non-	Dry	1	54.1	113.6	4.9	22
Degraded	Dry	2	56.8	103.6 (reg.)	4.8	33
	Dry	3	63.6	148.75	7.5	24
non-	Rainy	4	54.7	114.7	4.8	24
Degraded	Rainy	5	62.5	118.6	6.1	26
	Rainy	6	61.9	66.3 (reg.)	6.5	22
Degraded	Dry	7	56.4	113.8	5.4	26
	Dry	8	62.5	66.7 (reg.)	7.4	33
	Dry	9	63.2	157.3	7.7	32
	Dry	10	58.6	137.1	5.1	21
Degraded	Rainy	11	58.9	75.1 (reg.)	6.1	30
	Rainy	12	61.5	114.1	6.2	20
	Rainy	13	59.5	84.2 (reg.)	6.1	24

Radio tracking started only one day after capture so as to reduce any irregular behaviour resulting from capture. Animals were located five times a day (7.00am, 9.30am, 12.00pm, 3.00pm & 5.30pm). We kept sampling intervals of two and half hours because Hansteen et al. (1997) showed that sampling intervals of 160 minutes yielded uncorrelated data for area estimates. The larger sampling interval at noon accounted for an inactive period of the lizards during the hottest time of the day. An overview of numbers of bearings, body weight and dimensions of each lizard can be found in table 2. Lizards were located via RX 98 Televilt receiver (Televilt, Sweden) with a built in, directional antenna. We located transmitter fitted lizards by sweeping the tip of the antenna sidewise until the strongest signal was received and getting cautiously closer to the position of the lizards until the lizard could be seen. To keep disturbance of the lizards to a minimum we inserted a small flag into the ground two meters north of the original position of the lizard. Flags were moved to the original position of the lizards on the following day. To estimate the position of each lizard bearing we measured distances to two fixed markers with known distance between both and calculated x/y co-ordinates for all lizard bearings.

3.4 Daily movement distances

We defined daily movement distances as the straight-line distance lizards moved within 24hours. For both habitats daily movement distances were calculated using the distance between consecutive lizard locations using the program ArcGis (Copyright © 1995-2007 ESRI, USA). The mean distance covered by the lizards between each location period (7.00am - 9.30am, 9.30am - 12.00pm, 12.00pm - 3.00pm, 3.00pm – 5.30pm & 5.30pm - 7.00am) was calculated and summed up to 24h (Table 3). The straight-line distances underestimate the actual distance moved by the lizards (Harris et al., 1990; Webb and Shine, 1997).

3.5 Home range size

To estimate home size we applied the Kernel estimator (Worton 1987, 1989). The Kernel estimator was chosen because it does not assume any underlying spatial distribution (Hansteen et al. 1997) and is a robust and unbiased area estimator (Boerger et al. 2006). As the smoothing parameter we adopted the least squares cross validation (h_{lscv}) for fixed kernel area estimates (Seaman and Powell 1996, Boerger et al. 2006). The 90% isopleth was used to estimate home range area as recommended by Boerger et al. (2006). Home range sizes were calculated with Animal Movement 2.0 (Hooge and Eichenlaub 1997) for ArcView GIS 3.2 (ESRI, California, USA). To estimate minimum sample size, the number of pooled lizard bearings separated for both grazing states were plotted against cumulative home range size (converted to percent of maximum home range size) (Harris et al. 1990, Kenward 2001). We used the numbers of points needed to describe 80% of the 90% Kernel area range asymptote (Rose 1982, Knapp 2000). Twenty-one bearings for non-degraded habitats and 19 for degraded habitats described 80% of the home range size which is considered as the minimum of bearings to adequately represent home range size (Rose 1982). Hence, lizards with less than 21 and 19 bearings respectively were omitted from the analysis.

3.6 Microhabitat preference

We analysed microhabitat preference of *P. lineoocellata* in both habitats (degraded and non-degraded) to test whether the lizards favour structure-rich microhabitats where plant diversity and perennial grass cover are high and annual grass and shrub cover low, over structure-poor microhabitats (low plant diversity and perennial grass cover and high annual grass and shrub cover). Therefore, we compared vegetation structure in 4x4m plots at lizard bearings with random plots of the same size within the enclosed area of the furthermost north-south and east-west lizard bearings. For each plot percent ground cover of all plant species was recorded. We further calculated mean values for perennial grass-, annual grass-, herbaceous-, shrub cover and plant diversity (Shannon Index).

3.7 Statistical Analyses

To test for differences between mean home range areas (Kernel method), mean distance that lizards move within 24h and mean microhabitat use were compared. For all the statistical analysis we applied t-Tests (Dytham 1999) (© SPSS Inc., Version 11.5). For all tests, a P-value of < 0.05 was regarded as statistically significant.

4. Results

During the radio tracking study, home range and movement data were collected for 13 individuals of *P. lineoocellata* with 337 bearings in total (Table 2) for two different habitats distinguished by different vegetation composition, cover and diversity.

4.1 Daily movement distances

No significant difference were found between dry and rainy seasons for daily movement distances of *P. lineoocellata* for each habitat (non-degraded: $T_5 = 0.347$; degraded: $T_6 = 0.382$) (Table 3). Therefore, we pooled data of both seasons for further analysis of daily movement distances. In degraded habitats *P. lineoocellata* moved greater distances within 24h than in non-degraded ($T_{12} = 0.002$, Figure 1).

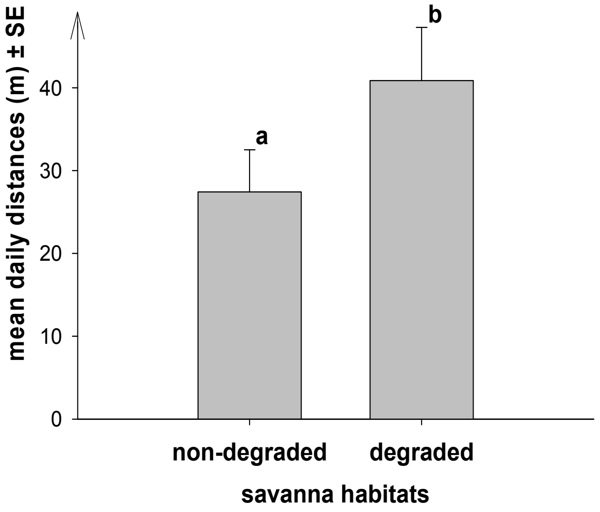

Figure 1 Daily movement distance (m) of *P. lineoocellata* (Means ± SE) in two savannah habitats (non-degraded vs. degraded). Different letters (a, b) indicate significant differences between the respective habitat (T-Test, p-value < 0.002).

Table 3 Home range size and daily movement distances in two savannah habitats (non-degraded vs. degraded) in dry and wet season.

Habitat type	Season	Lizard no.	distance (m/24h)	Home range (m²) (90% isopleth)
non-Degraded	dry	1	19.04	142.39
	dry	2	28.38	190.12
	dry	3	28.34	53.75
non-Degraded	rainy	4	26.43	212.34
	rainy	5	27.50	364.58
	rainy	6	34.90	291.72
Degraded	dry	7	31.69	507.62
	dry	8	36.03	485.10
	dry	9	43.82	591.69
	dry	10	43.89	509.15
Degraded	rainy	11	46.86	1181.60
	rainy	12	48.42	676.96
	rainy	13	35.48	574.38

4.2 Home range size

No significant difference between seasonal (dry vs. rainy season) home range size for both habitats (non-degraded and degraded) were found for the Kernel Method (non-degraded: $T_5 = 0.054$; degraded: $T_6 = 0.131$) (Table 3). Therefore, we can state that home range size for *P. lineoocellata* is not affected by seasons. For further home range analysis we pooled data of both seasons.

The statistical analysis of home range size revealed that there was a significant difference between non-degraded and degraded habitats (Kernel: $T_{12} = 0.002$). Home ranges of *P. lineoocellata* were significantly larger in degraded habitats than in non-degraded habitats (Figure 2).

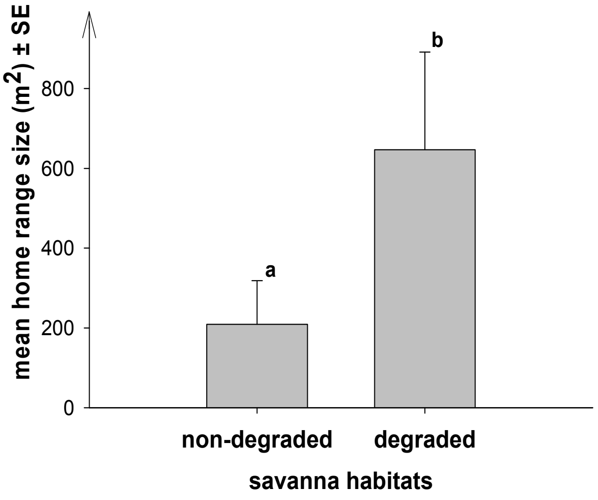

Figure 2 Home range size of *P. lineoocellata* (Means ± SE) in the two savannah habitats (non-degraded vs. degraded). Different letters (a, b) indicate significant differences between the respective habitat (T-Test, p-value < 0.002).

4.3 Microhabitat preference

Table 4 displays vegetation cover (perennial grass, annual grass, herbs and shrubs) and plant diversity for microhabitats of lizard bearings compared to random plots in both habitats. We found no difference in microhabitat use of *P. lineoocellata* for non-degraded habitats (perennial grass: $T_5 = 0.121$; annual grass: $T_5 = 0.146$; shrubs: $T_5 = 0.798$; herbs: $T_5 = 0.819$; plant diversity: $T_5 = 0.957$) (table 4). In contrast, in degraded habitats, *P. lineoocellata* preferred microhabitats with higher plant diversity ($T_6 = 0.042$), higher perennial grass cover ($T_6 = 0.028$), lower annual grass cover ($T_6 = 0.011$) and lower shrub cover ($T_6 = 0.002$) within its home range (table 4).

Table 4 Mean vegetation cover of perennial grasses, annual grasses, herbs and shrubs for lizard bearing and random microhabitats of *P. lineoocellata* in two savannah habitats (non-degraded vs. degraded).

	non-degraded habitats				degraded habitats			
	vegetation cover (%)				vegetation cover (%)			
	lizard bearing	random	T-value	P-value	lizard bearing	random	T-value	P-value
perennial grass	33.56	35.46	-1.69	0.121	10.94	6.77	2.49	0.028
annual grass	1.61	0.88	1.58	0.146	8.59	14.25	-2.99	0.011
herbs	3.31	3.6	-0.24	0.819	1.34	1.43	-0.11	0.914
shrubs	0	0	0.26	0.798	10.6	15.37	-3.91	0.002
plant diversity	0.65	0.65	0.055	0.957	0.59	0.5	2.28	0.042

5. Discussion

The results of the radio tracking study of *Pedioplanis l. lineoocellata* document the significant impact of habitat degradation in savannahs on space use. Home range size and daily distances the lizard moved were larger in degraded habitats (low plant diversity and perennial grass cover and high shrub and annual grass cover) compared to non-degraded habitats (high plant diversity, high perennial grass and low shrub cover). Moreover, in degraded habitats where the structural diversity of the vegetation per se is low, the lizards preferred microhabitats of higher structural diversity (high plant diversity, high perennial grass cover and low shrub cover) within their home range.

5.1 Daily movement distances

Travelling longer distances in the search of prey in degraded habitats reduces the amount of time that can be spent on other important daily activities (e.g. thermoregulation) and can also enhance predation risk (Munger et al. 1983, Wymann and Whiting 2002). When covering greater distances the exposition to predators increases, especially in areas where vegetation cover is low. Even if the lizards try to compensate the duration of travel by moving faster it has several negative effects. Moving faster results in a higher expenditure of energy (Pérez-Tris et al. 2004, Amo et al. 2007) which leads to an increase in food demand. This is particularly problematic in degraded habitats, where prey availability is already low (Seymour and Dean 1999, Blaum et al. in press, see Chapter 1 and 2).

5.2 Home range size

As compensation to depleted food resources in degraded savannah habitats (Gandar 1982, Dean & Milton 1995, Seymour and Dean 1999) the lizard *Pedioplanis l. lineoocellata* increases both its search activity and also increases home range size (Knapp and Owens 2005). Optimal foraging theory suggests that animals can adapt home range size according to local food resources (MacArthur and Pianka 1966, Wauters and Dhondt 1992, Powell et al. 2000). Rodents for example can enlarge their home ranges when food resources become scarce (Tait 1981 (Deermice, *Peromyscus maniculatus*); Tait and Krebs 1981(voles, *Microtus townsendi*)). Also, lizards adapt their home range size in relation to food availability (this study; Simon 1975; Ruby and Dunham 1987). While we found an increase in home range size for *P. lineoocellata* when food availability is low, *Sceleporus species* decrease their home range size as a response to increased food availability (Simon 1975; Ruby and Dunham 1987). Clearly, food availability is one major determent of local species abundance.

Therefore, we expected that the sit and wait foraging strategy of *P. lineoocellata* (Branch 1998) limits the occurrence of the lizard to habitats where food availability is high, i.e. non-degraded savannah habitats. Or in other words, we expected the local absence of *P. lineoocellata* in resource-poor degraded habitats. Interestingly, although food availability in degraded habitats was low, the lizard occurred in these food- and vegetation structure-poor savannah habitats. The strong increase in daily movement distances in degraded habitats suggests a behavioural flexibility of the lizard's space use. In degraded habitats, *P. lineoocellata* changed its foraging strategy from sit and wait to actively foraging (see Chapter 2).

An increase in home range size in degraded habitats may result in smaller population sizes because each individual needs more space to meet its daily life requirements: Fewer individuals of *P. lineoocellata* occupy the same area. However, the increase in home range size could be compensated by an increase in home range overlap. For *P. lineoocellata* such increase in home range overlap is highly unlikely that the species can fully compensate the increase of home range size with home range overlap because home range size increases from non-degraded (home range size: 209.15 m^2) to degraded habitats (646.64m^2) by more than threefold. This is supported by lower absolute population densities of *P. lineoocellata* in degraded habitats (see Chapter 1).

5.3 Microhabitat preference

In degraded savannah habitats *P. lineoocellata* favours structural diverse microhabitats inside home ranges that are poor in vegetation structure. This preference can be explained by local variations in prey availability at microhabitat scale. Even in degraded habitats prey abundance is higher in structural rich microhabitats than in the structural poor surrounding. Another advantage of favouring structural rich microhabitats is the larger amount of vegetation cover that effectively protects *P. lineoocellata* from predators (Castilla and Bauwens 1991; Bentley et al. 2000, Norbury 2001). This is further supported by a study on Northern Alligator Lizards (*Elgaria coerulea*) and Western Skinks (*Eumeces skilonianus*) where the removal of cover was detrimental to both species (Rutherford and Gregory 2003).

Nevertheless, as discussed above, the increase in daily movement activities in degraded habitats results also in a higher predation risk (Huey and Pianka 1981, Polis 1988, Wymann and Whiting 2002). High vegetation cover, particularly of perennial grass tussocks in non-degraded areas offer better protection from predators, because the moving lizards are less likely to be seen when moving through open areas (Kearney et al. 2007). Also, higher structural diversity and vegetation cover offers more escape sites and refuges which additionally reduce predation risk (Fox 1978, Civantos 2000). Fox (1978) showed that habitat quality in regard to vegetation cover and diversity influenced survival of the lizard *Uta stansburiana* positively, whereas a loss of vegetation and plant diversity increased mortality.

5.4 Conclusions

Although the type of foraging mode is linked to morphological traits (Anderson and Karasov 1988, Wymann and Whiting 2002), *P. lineoocellata*, however, changes its foraging mode in response to low food availability. This behavioural flexibility suggests that the species can buffer the negative impact of habitat degradation and enables the species to use and survive in degraded savannahs.

Nevertheless, the demonstrated increase in home range size coupled with a possible higher predation risk may also lead to local extinction of *P. lineoocellata* in degraded savannah habitats. Also in the ecotone of short-grass prairie and Chihuahuan Desert (USA) vegetation cover and structural diversity determined the survival of the lizard *Uta stansburiana,* and a loss of vegetation cover and plant diversity increased the lizard’s mortality (Fox 1978). Our conclusion is also supported by an earlier study on *P. lineoocellata*, where population densities in degraded savannah habitats were significantly lower compared to non-degraded habitats (see Chapter 1).

For future research we suggest to focus on behavioural adaptations in response to habitat degradation, especially under recent climatic changes. Climate change scenarios for southern African sub region predict a 10-15% decrease in mean annual rainfall together with a rise in daily temperatures (UNEP-IPCC4-Report 2007) which will affect vegetation cover, composition and animal taxa across all trophic levels. Behavioural flexibility and adaptations may then become increasingly important for the survival of species and also for the development of management strategies under the predicted climatic changes in arid and semiarid environments.

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Link to chapter four

The results of chapter three showed that habitat degradation caused by overgrazing negatively affected one of the major aspects of *P. lineoocellata* life history, the space use. Home range was significantly increased in degraded habitats. Despite these important findings, nevertheless, it remains unclear how changes in space use under changes in habitat quality affect population viability. Therefore, I analysed relevant parameters of population dynamics of *P. lineoocellata* in chapter 4. Using capture-mark-recapture I determined absolute population size, fitness, survival rate, birth rate, predation risk and sex ratio as important population parameters. With this additional information I discuss the potential of *P. lineoocellata* in Kalahari savannahs to be part of metapopulation dynamics (in the sense of Hanski 1998) or part of source-sink dynamics (Boughton 1999) i.e. degraded habitats acts as population sinks and depend on non-degraded habitats as population sources.

Boughton D.A. (1999) Empirical evidence for complex source-sink dynamics with alternative states in a butterfly metapopulation. Ecology 80: 2727-2739

Hanski I (1998) Metapopulation dynamics. Nature 396: 41-49

Chapter 4

Consequences of habitat degradation for the population dynamics of the lizard *Pedioplanis l. lineoocellata*in the southern Kalahari

Consequences of habitat degradation for the population dynamics of the lizard *Pedioplanis l. lineoocellata* in the southern Kalahari [1]

1. Abstract

In southern Kalahari savannah rangelands shrub encroachment as a consequence of overgrazing has become increasingly evident over the past decades. Shrub encroachment has lead to substantial changes in plant diversity, composition, vegetation cover and structure affecting resource availability (e.g. food, predation cover) and resources use across a variety of animal taxa. While shrub encroachment reduces animal diversity across taxa our knowledge of the effects of shrub encroachment on populations dynamics of reptiles remain poor. Using capture-mark-recapture we investigated population size, survival rate, birth rate and predation risk of the *Pedioplanis l. lineoocellata* (Spotted Sand Lizard) in degraded versus non-degraded savannah habitats. In non-degraded habitats plant diversity and the proportion of perennial grass cover was high, and shrub cover was low, while in degraded habitats plant diversity and perennial grass cover was low, and proportion of shrub cover was high. Our results show that in degraded habitats absolute population size, survival rate, birth rate was significantly lower and ion addition, predation risk was significantly higher. We suggest that reduced prey availability, vegetation cover and vegetation structure in degraded habitats are responsible for these changes of population parameters. As a consequence we conclude that overgrazing has a severe impact on the population dynamic of *P. lineoocellata* and hence on the long-term survival in degraded habitats.

2. Introduction

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[1] This chapter is the final stage of preparation:

Wasiolka B., Blaum N., Henschel J. and Jeltsch F.: Consequences of habitat degradation for the population dynamics of the lizard *Pedioplanis l. lineoocellata* in the southern Kalahari

In the last decades anthropogenic land use has altered vegetation composition and structure in savannah ecosystems (e.g. Archer et al. 1995, Jeltsch et al. 1996, Roques et al. 2001, Sankaran et al. 2005). High grazing pressure especially by domestic livestock (Jeltsch et al. 1991, Roques et al. 2001) usually causes overgrazing. Increase of shrubby vegetation (Skarpe 1990, Teague and Smit 1992 and Jeltsch et al. 1997) at the cost of perennial grasses and herbaceous vegetation (Van Auken 2002, Wiegand et al. 2005) can lead to degraded habitats, in the worst cases to shrub encroachment over wide areas or to desertified habitats, respectively (e.g. Skarpe 1991; Teague and Smit 1992; Jeltsch et al. 1997). These resulting changes alter vegetation structure and composition in a way that structural diversity declines (Tews et al. 2004). Changes in vegetation structure, composition and cover caused by overgrazing can alter environmental conditions such as the availability of resources (Saunders et al. 1991) or cover (safe sites) (Huey and Pianka 1981, Martín and López 1999) for a variety of species. In consequence, living conditions in savannah ecosystems change for a variety of animal taxa, resulting in a decline of faunal abundance and diversity (e.g. Seymour and Dean 1999, Blaum et al. 2007a, 2007b Thiele et al. in press). Despite concerns over the influence of habitat degradation on population density, the absolute abundances of affected reptile populations are rarely studied. It is of importance to know the impact of habitat degradation on absolute abundance and not only of relative abundance to estimate the direct losses of species abundance in order to elucidate survival of small sub populations. Furthermore, it is of importance to investigate if other factors of population dynamics like condition, survival and birth rate are likewise affected by habitat degradation.

Hence, we conducted a capture-mark-recapture study of the Spotted Sand Lizard, *P. lineoocellata*, a medium sized, diurnal, ground dwelling lizard (Branch 1998), across a range of habitats which differ in vegetation composition and structural diversity to estimate population size, survival and birth rate and other population parameters. Non-degraded habitats are characterized by high perennial grass cover, low shrub cover and high plant diversity and degraded habitats by low perennial grass cover, high shrub cover and plant diversity.

We addressed the following hypotheses: (1) Absolute population size of *P. lineoocellata* decrease with intensity of habitat degradation; (2) Because of reduced structural diversity and vegetation cover predation risk is increased and hence survival rate and condition is lower in non-degraded habitats; (3) As a consequence of increased predation risk and decreased survival rate the birth rate is lower in degraded habitats.

3. Methods

To investigate the response of *Pedioplanis l. lineoocellata* to habitat degradation we conducted a capture-mark-recapture study to estimate population parameters like population size, survival rate, sex ratio, fecundity, predation risk and condition.

3.1 Study area

Our study of *Pedioplanis l. lineoocellata* was conducted on the farms “Loch Lemond” (S 27°02’; E 20°44’), “Rooiduin” (S 26°42’; E20°35’) and “Swartpan” (27°15’; E20°46’) in the southern Kalahari, South Africa, close to the Kgalagadi Transfrontier Park.
The semi-arid savannah of the Kalahari is characterized by a continuous grass layer (e.g. *Centropodia glauca, Stipagrostis uniplumis, S. ciliata*) and a discontinuous woody layer consisting of trees (e.g. *Acacia erioloba, A. haematoxylon* and *Boscia albitrunca*) and shrubs such as e.g. *Acacia mellifera*, *Lycium hirsutum* and *Rhigozum trichotomum* (Acocks 1988, van Rooyen, 2001). The region receives an annual rainfall of 150 to 350mm (van Rooyen, 2001) which falls mainly in the summer month (Werger, 1978). Temperature extremes range from winter lows reaching –10.3 °C to summer highs up to 45.4 °C (van Rooyen 2001).

3.2 Capture-Mark-Recapture

The study was performed in three different habitat types differing within their grazing conditions. This gradient is characterized by a decrease of perennial grasses and herbaceous plants and an increase of annual grasses and shrubs. Vegetation was classified according to composition and diversity (Table 1).

Table 1 Range of vegetation cover of shrub, perennial grass, annual grass, herb, bare ground and diversity index (H’) for the three vegetation states

Vegetation state	Vegetation cover (%)					Diversity Index (H’)
	Shrubs	Perennial grass	Annual grass	Herbs	Bare ground	
vegetation state 1	0-1	31-38	0-1	2-5	57-65	0.72
vegetation state 2	0-1	19-30	4-7	1-5	61-72	0.78
vegetation state 3	13-18	3-9	7-12	0-2	65-76	0.51

We applied the “Robust Design” (Pollock 1982, Kendall and Pollock 1992, Kendall et al. 1997, Williams et al. 2002) because it is robust to heterogeneity and trap response (Pollock 1982) and enables one to estimate the most parameter (e.g. population size, survival rate) (Kendall and Pollock 1992). Following the “Robust Design” this study consisted of three primary periods (March/April 2005, November/December 2005 and February-April 2006) of trapping for each of the three grazing states. For each vegetation state the trapping was replicated three times. The Spotted Sand Lizard population was expected to be open to gains and losses between the primary periods. The secondary periods within each primary period consisted of nine consecutive capture days, and the population was assumed to be closed to gains and losses among the secondary periods.

We analysed our data set using a two-stage analysis following Pollock (1982). First, population size was estimated using closed-population models with capture history data across secondary periods within each primary period. Then, survival was estimated by combining data across secondary periods to indicate whether or not a lizard had been caught at least once during a primary period. The resulting capture histories were evaluated by open models across all primary periods.

3.3 Trap design

Within the three different habitats (vegetation state 1-3) we set up a standard reptile sampling array composed of a combination of buckets and drift fences (Heyer et al. 1994). Within a 40 by 40 meter square, a sampling array contained a total of 16 drift fences (each 8m long) and 32 buckets were placed (10litres) (Figure 1). To minimize heat stress and predation risk of captured lizards traps were checked four times a day (6.30; 11.30; 14.30; 17.30 hours). All specimen of *P. lineoocellata* were marked, sexed (only adults), and checked for tail loss. We measured body weight (g), snout-vent length (mm) and tail length (mm). Toe clipping after a predefined code (maximum of two toes on two different feet) was applied to identify individuals in the following primary periods (Henle et al. 1997). To minimize lizards harm, toe clipping was not done in the third and last primary period. Instead of toe clipping each specimen was marked using a xylene free paint-marker (Boone & Larue 1999). At the Port Elizabeth Museum, South Africa, clipped toes were used for genetic analysis.

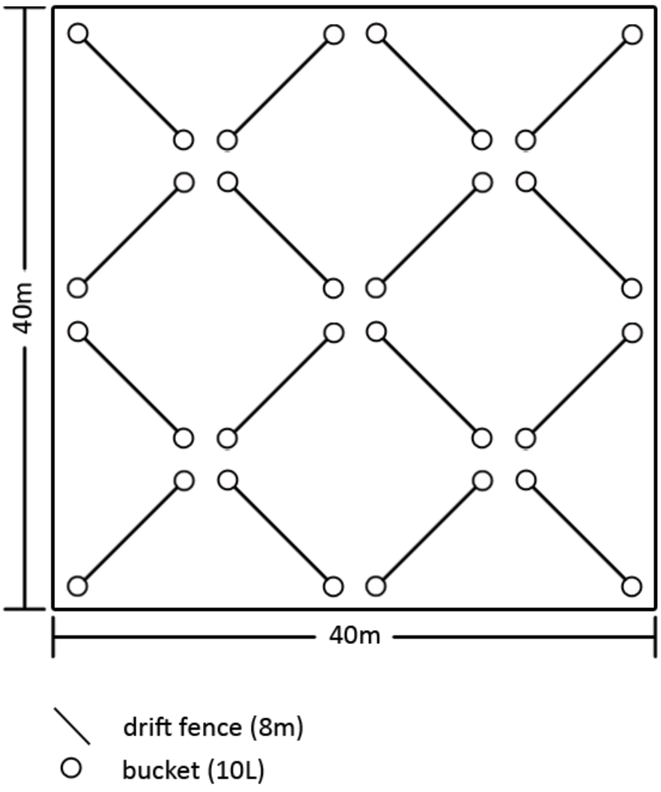

Figure 1 Sampling array for the capture-mark-recapture of *Pedioplanis l. lineoocellata*

3.4 Size Classes

For all captured Spotted Sand lizards except gravid females or individuals with lost or regenerated tails we plotted snout-vent-length versus body mass in order to identify size classes. Recaptured specimen were incorporated only once into the analysis.

3.5 Population size

To estimate population size we used the CAPTURE package of the program MARK (Otis et al. 1978, White & Burnhem 1999). We investigated capture probabilities by assessing the model selection of four likely models (Otis et al. 1978): M_0 (constant capture probability), M_h (capture probability heterogeneous among individuals), M_{bh} (behavioural response in capture probability with heterogeneity among individuals), M_{tbh} (capture probability affected by secondary sampling period, trap response and heterogeneity). Population size of adults and juveniles was calculated separately. As estimations for limited dataset were not possible, we estimated population size for all primary periods with less than three individuals captured by using a calibration line. This calibration line was established by plotting the estimated population size data of appropriate data sets (y-axis) against the numbers of individuals caught (x-axis).

3.6 Survival rate

The estimates for survival were also calculated with MARK (White & Burnhem 1999). It allows fitting different Cormack-Jolly-Seber (CJS) models to capture-mark-recapture data to determine the most appropriate model. Model selection was based on the corrected Akaike Information Criterion (ΔAICc) (). The best model with the lowest AICc is regarded to be the most parsimonious model (Anderson et al. 1994). The following six models were considered (following the notation of Pollock et al. 1990): {Φ(.) p(.)}, {Φ(.) p(t)}, {Φ(t) p(t)}, {Φ(t) p(.)}, {Φ(.) p(p)} and {Φ(t) p(p)} (notation: Φ: survival rate, p: capture probability, (.): constant parameter across time, (t): time-specific parameters, (p): estimated capture probabilities of the second and third secondary session). For further analysis the survival rates were expressed on an annual basis. We omitted juveniles from the estimation of survival as the recapture rate of juveniles was very low in the following periods.

3.7 Sex ratio

For all vegetation states we calculated lizard sex ratios (S, males vs. females) using all adult males and females of the three primary periods. In the analysis recaptured males and females were included only once.

3.8 Fecundity

To determine fecundity we calculated the average birth rate (number of juveniles, (N_j) per number of females, (N_F)) for each vegetation state. The population size of females was assessed by applying the sex ratio to the estimated population size of adults (N_A): $N_F=N_A/(S+1)$.

3.9 Predation risk

To estimate the predation risk for each vegetation state we assessed the proportion of all captured specimen who had lost their tail or part of it in each habitat. Recaptured individuals were considered only once. Lizards use caudal autotomy as a defence or escape mode against predators (e.g. Martin & Salvador 1992, Fox & McCoy 2000). Therefore, the lack of tails and can be used as a surrogate for predation risk.

3.10 Condition

Condition was determined by the body mass – snout-vent length ratio (BSR). Body mass in mg was divided by Snout vent length (SVL) in mm. The ratios for males, females and juveniles were calculated separately. Individuals with caudal autotomy were omitted from the analysis and recaptured individuals were incorporated into the analysis only once.

Condition was determined by calculating a body mass – length index. Hence, we compared body mass per 1mm SVL of *P. lineoocellata* for the three vegetation states. The body mass – length index for males, females and juveniles were calculated separately. Individuals with caudal autotomy were omitted from the analysis and recaptured individuals were incorporated into the analysis only once.

3.11 Statistical Analyses

To test for differences among grazing states we compared population sizes (adults and juveniles), survival rate (adults), mean sex ratio, mean fecundity, mean predation risk and mean condition using a one-factor ANOVA (Dytham 1999) using SPSS 11.5 (SPSS Inc., Chicago, Illinois). When the ANOVA indicated significant differences we compared individual means between different grazing states using Tukey's post-hoc-test. For each test, a P-value of < 0.05 was regarded as statistically significant.

4. Results

4.1 Size class

The graph of the size classes (Figure 2) showed two separate scatter-plots. Hence, we tested for significant differences between size classes with an analysis of covariance. We referred to the scatter-plot on the bottom left corner as size class 1 and to the top right as size class 2. The ANCOVA using size class as the grouping variable (factor), log snout-vent-length (SVL) as the dependent variable and body mass as the covariate show that there is a significant difference between the two size classes ($F_{1.364}$ = 12.03, P = 0.001). Therefore we refer in the following to size class 1 as juveniles and to size class 2 as adults.

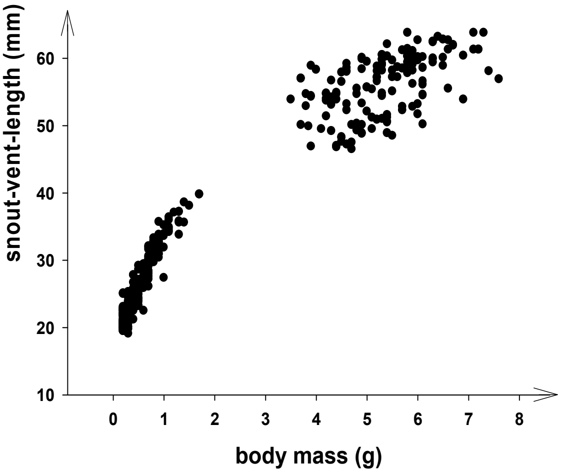

Figure 2 Snout vent length (SVL) versus body mass of *Pedioplanis l. lineoocellata*

4.2 Population size

Among the four top models receiving the highest model selection scores, the constant-parameter model, M_0, was selected for most of the data sets (Table 2). To ensure comparability within the data sets we chose to use model M_0 to estimate population size of adults and juveniles for all data sets. Absolute population sizes of *P. lineoocellata* for adults and juveniles differed significantly among vegetation states (adult: $F_{2.6} = 20.212$, $P = 0.002$; juvenile: $F_{2.6} = 13.613$, $P = 0.006$). The post-hoc test showed that population sizes of adults and juveniles were significantly larger in vegetation states 1 and 2 than in vegetation state 3 (Figures 3 & 4). A detailed overview of the population size of adult and juvenile *P. lineoocellata* for all primary periods and vegetation states are given in Table 3.

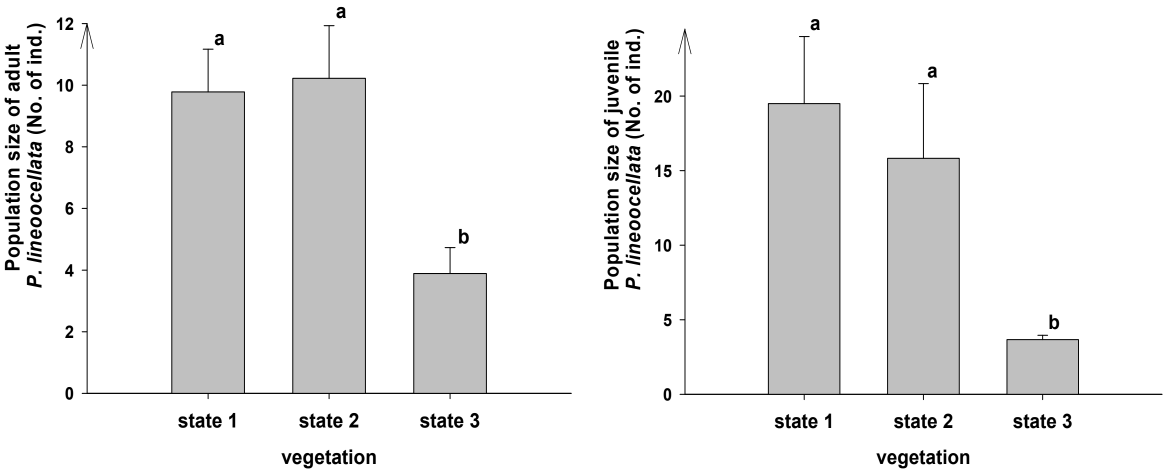

Figure 3 & 4 Means ± SE of the population size of (3) adult and (4) juvenile *Pedioplanis l. lineoocellata* in three different habitats. Different letters (a, b) indicate significant differences between the respective vegetation state (ANOVA, Tukey Post Hoc Test, p-value < 0.05).

Table 2 Model selection statistics based on *Pedioplanis l. lineoocellata* mark-recapture data for adults and juveniles for the three vegetation states

Vegetation state	Location	Primary period	Model score adult				Model score juveniles			
			M_0	M_h	M_{bh}	M_{tbh}	M_0	M_h	M_{bh}	M_{tbh}
1	Swartpan	1	1	0.9	0.96	0.96	0.49	0.02	0.45	0.34
		2	1	0.8	0.68	0.78				
		3	1	0.79	0.6	0.69	1	0.93	0.9	0.96
1	Rooiduin	1	1	0.79	0.58	0.71	0.87	0.97	0.17	1
		2	1	0.93	0.98	0.97				
		3	1	0.81	0.66	0.73	1	0.55	0.75	0.89
1	Loch Lemond	1	0.96	1	0.58	0.73	1	0.82	0.56	0.63
		2	0.99	1	0.85	0.92				
		3	0.98	1	0.96	0.87	1	0.75	0.75	0.85
2	Swartpan 1	1	1	0.82	0.62	0.7	1	0.9	0.72	0.82
		2	0.15	0	0.32	0.58				
		3	0.93	0.8	1	0.98	1	0.95	0.59	0.66
2	Swartpan 2	1	1	0.81	0.6	0.66	1	0.82	0.57	0.76
		2	1	1	0.59	0.73				
		3	0.55	0.37	0.9	1	1	0.84	0.7	0.99
2	Loch Lemond	1	1	0.91	0.66	0.71	0.89	0.97	0.27	1
		2	1	0.87	0.59	0.66				
		3	0.96	0.88	1	0.97	1	0.87	0.6	0.69
3	Rooiduin 1	1	0.77	0.62	1	0.98	1	0.89	0.68	0.7
		2	1	0.97	0.78	0.78				
		3	1	0.91	0.68	0.71	1	0.82	0.6	0.68
3	Rooiduin 2	1	1	0.89	0.55	0.59	0.92	1	0.26	0.68
		2	0.47	0.16	0.39	0.52				
		3	1	0.81	0.59	0.67	1	0.85	0.63	0.67
3	Loch Lemond	1	-	-	-	-	-	-	-	-
		2	1	0.85	0.58	0.62				
		3	1	0.84	0.59	0.66	1	0.85	0.63	0.68

Notes: Analyses were performed using the Program MARK separately for the secondary sampling periods within each primary period. The models are: M_0: constant capture probability, M_h: capture probability heterogeneous among individuals, M_{bh}: behavioural response in capture probability with heterogeneity among individuals, M_{tbh}: capture probability affected by secondary sampling period, trap response and heterogeneity.

Table 3 Estimated population size of adult and juvenile *Pedioplanis l. lineoocellata* for the three vegetation states calculated after the M_0 Model with the program MARK (CAPTURE-Package)

Vegetation state	Location	Primary period	Population size adults $N(a)_t$	Population size juveniles $N(j)_t$
1	Swartpan	1	8 (0.4)	16 (0.93)
		2	10 (0.01)	-
		3	8 (0.55)	14 (10.49)
1	Rooiduin	1	10 (0.65)	28 (23.37)
		2	10 (0.94)	-
		3	8 (0.49)	20 (0.90)
1	Loch Lemond	1	9 (0.83)	12 (10.44)
		2	18 (16.12)	-
		3	7 (0.46)	27 (12.35)
2	Swartpan 1	1	9 (0.48)	16 (10.64)
		2	13 (0.88)	-
		3	10 (0.71)	12 (0.798)
2	Swartpan 2	1	9 (0.63)	13 (10.45)
		2	15 (10.56)	-
		3	11 (0.67)	11 (0.73)
2	Loch Lemond	1	6 (0.65)	20 (14.68)
		2	12 (0.45)	-
		3	7 (0.46)	23 (10.49)
3	Rooiduin 1	1	5 (0.27)	4 [1]
		2	4 (0.43)	-
		3	3 [1]	5 (0.46)
3	Rooiduin 2	1	5 (0.46)	4 (11.29)
		2	5 (0.13)	-
		3	4 (0.35)	4 [1]
3	Loch Lemond	1	2 [1]	2 [1]
		2	4 (0.43)	-
		3	3 [1]	6 (0.43)

Values in brackets are estimated standard errors

[1] Values estimated by calibration line

4.3 Survival rate

In the majority of the cases the model {Φ(.) p(fix)} (constant survival rate over the secondary periods and fixed capture probabilities) yielded the best results (lowest AICc) (Table 4). Thus, we decided to apply this model to all cases. The ANOVA revealed no significant difference ($F_{2.6}$ = 2.445, P = 0.167) among the three vegetation states for the annual survival rate. Nevertheless, the results clearly indicate a higher annual survival rate in vegetation state 1 & 2 than in state 3 (state1: Φ = 0.38 & state 2: Φ = 0.45 vs. state 3: Φ = 0.05) (Figure 5)

Table 4 Estimated survival rates of adult *Pedioplanis l. lineoocellata* for the three vegetation scenarios.

State	Location	Model description	AICc	ΔAICc	AICc weight	Monthly survival estimate	Annual survival estimate
1	Swartpan	{Φ(.) p(p)}	27.17	0	0.33	0.97 (0.00)	0.71 (2.38E-28)
	Rooiduin	{Φ(.) p(p)}	19.59	0	0.51	0.85 (0.07)	0.14 (2.55E-14)
	Loch Lemond	{Φ(.) p(p)}	30.04	5.35	0.03	0.90 (0.06)	0.29 (2.53E-15)
2	Swartpan 1	{Φ(.) p(p)}	31.05	0,51	0.17	0.96 (0.05)	0.61 (3.99E-16)
	Swartpan 2	{Φ(.) p(p)}	26.06	0	0.38	0.84 (0.07)	0.13 (2.03E-14)
	Loch Lemond	{Φ(.) p(p)}	25,1	0	0.29	0.96 (0.05)	0.61 (3.04E-16)
3	Rooiduin 1	{Φ(.) p(p)}	7,98	0.91	0.21	0	0
	Rooiduin 2	{Φ(.) p(p)}	10.72	3.21	0.06	0.75 (0.15)	0.031 (1.19E-10))
	Loch Lemond	{Φ(.) p(p)}	3.0	0	0.75	0.84 (0.10)	0.12 (9.84E-13)

Values in brackets are estimated standard errors
Φ: survival rate
(.): constant parameter across time
(t): time-specific parameters
(p): estimated capture probabilities of the second and third secondary session

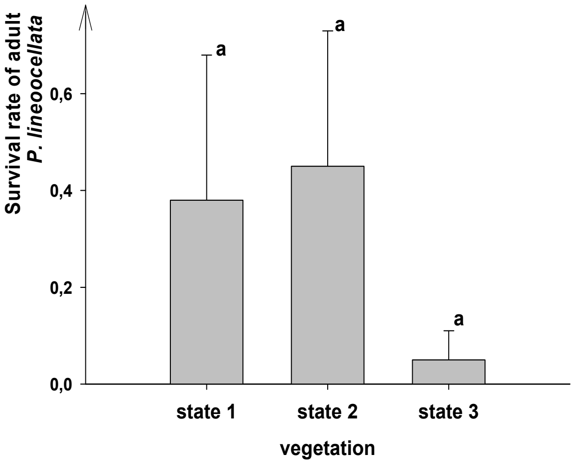

Figure 5 Means ± SE of the annual survival rate of adult *Pedioplanis l. lineoocellata*) in the three different habitats. Same letter (a) indicate no significant differences between the respective vegetation state (ANOVA, Tukey Post Hoc Test, p-value < 0.05).

4.4 Sex ratio

Among the three vegetation states we found no significant difference ($F_{2.6}$ = 1.004, P = 0.421) for the sex ratios (Table 5).

Table 5 Sex ratio (males : females), fecundity (no. of juveniles per female), predation risk (tail loss, %) and condition (body mass–snout vent length ratio) for males, females and juveniles for the three vegetation states

Vegetation State	sex ratio ♂ - ♀	Fecundity No. of juv. per female	Predation risk - tail loss (%)	Condition body mass per SVL (mg/mm) males	females	juveniles
vegetation state 1	1.10	4.71	7.02	9.65	8.84	1.06
vegetation state 2	0.89	4.75	9.19	10.65	9.39	1.81
vegetation state 3	0.98	2.14	24.60	8.92	8.96	1.54

4.5 Fecundity

The statistical analysis displayed a significant difference ($F_{2.6}$ = 7.168, P = 0.026) among birth rates (no. of juveniles per female) for the three vegetation states. The Tukey-Test displayed that the birth rate at vegetation state 3 was significant lower than at the two other states (Figure 6, Table 5).

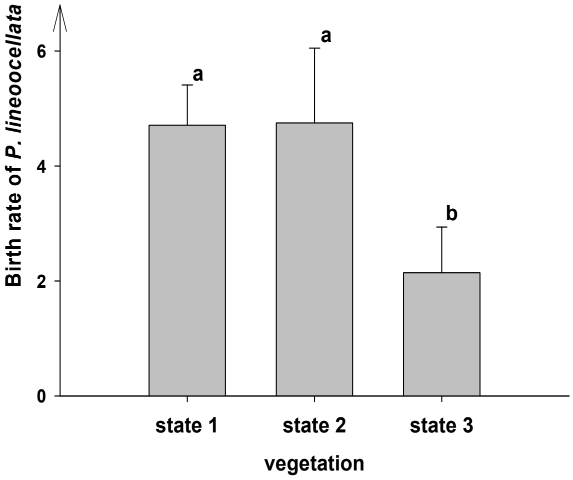

Figure 6 Means ± SE of birth rates (number of juveniles per female) of *Pedioplanis l. lineoocellata*. Different letters (a, b) indicate significant differences between the respective vegetation state (ANOVA, Tukey Post Hoc Test, p-value < 0.05).

4.6 Predation risk

The results of the predation risk analysis showed a significant ($F_{2.6}$ = 206.45, P < 0.001) difference among the vegetation states. The Tukey-test revealed that the predation risk in vegetation state 3 habitats was significantly higher than in the two other habitats (Figure 7, Table 5).

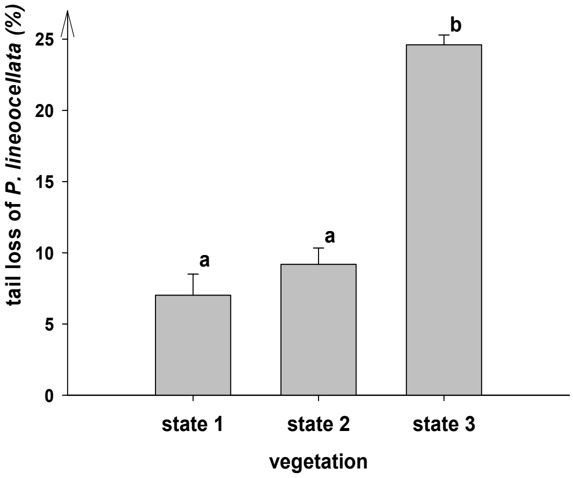

Figure 7 Means ± SE of tail loss of *Pedioplanis l. lineoocellata* (%) as an indicator of predation risk for the three vegetation states. Different letters (a, b) indicate significant differences between the respective vegetation state (ANOVA, Tukey Post Hoc Test, p-value < 0.05).

4.7 Condition

The test of condition (body mass – length index) in the three vegetation states demonstrated a significant difference only for condition of adult male ($F_{2.6}$ = 11.929, P = 0.008) but not for adult females ($F_{2.6}$ = 0.457, P = 0.654) or juveniles ($F_{2.6}$ = 0.826, P = 0.482) (Table 5). The post-hoc test showed that condition of adult males were significantly greater in vegetation state 2 than in vegetation state 3, while condition in vegetation state 1 was intermediate and not significantly different from the other two states (Table 5).

5. Discussion

Our results clearly show that habitat degradation has severe negative effects on the population dynamics of the Spotted Sand Lizard, *Pedioplanis l. lineoocellata*. Most of the investigated parameters discussed below show a significant negative influence of degradation, none show any positive influence. The three most important parameters, population size of adults and juveniles and female fecundity were significantly lower in degraded habitats (vegetation state 3) compared to non-degraded habitats (vegetation state 1 and 2). Furthermore, predation risk of adult *P. lineoocellata* is greatly enhanced in degraded habitats. While the condition (body mass – snout-vent length ratio (BSR)) of males was lower in vegetation state 2 and 3 there was no significant difference in condition of females and juveniles among vegetation states. Habitat degradation did not affect sex ratio.

The sex ratio by *P. lineoocellata* of close to 1:1 in all three vegetation states indicates that disturbance did not affect factors related to this parity. A sex ratio of lizards close to 1:1 are found over a wide range of species, locations, habitats and age classes (e.g. Ortega-Rubio et al. 2000, Van Sluys 2000, Capula et al. 2002, Gruber 2002, Lemos-Espinal et al. 2003, Mouton et al. 2005).

The decline in absolute population size of juvenile and adult Spotted Sand Lizards in degraded habitats (vegetation state 3) can be explained by the loss of vegetation cover coupled with a decline in prey availability (Van Vuren and Coblentz 1987, Fleischner 1994, Blaum et al. in press, see Chapter 1 and 2). First, low proportion of perennial grass and herbaceous vegetation cover together with low plant diversity in degraded savannah habitats can also lead to a reduction of prey availability (Gandar 1982, Dean and Milton 1995, Blaum et al. in press). In contrast, higher abundance of prey in non-degraded savannah habitats supports higher faunal abundance (Steenkamp and Chown 1995, Seymour and Dean 1999). An increase of home range size is a possible compensatory mechanism to low prey availability in degraded habitats (Wauters and Dhondt 1992, Knapp and Owens 2005). An increase in home range size in degraded habitats implies that population densities of *P. lineoocellata* decline if the species does not compensate this increase by an increase in home range overlap; since each individual needs more space to meet its dietary demands (see Chapter 3). As a response to reduced prey availability in degraded habitats, birth rates (no. of juveniles per female) were significantly lower in degraded areas than in non-degraded areas.

We also expected that prey availability to influence reptile condition (BSR) and fecundity. However, we only found a significant difference of male condition between males of state 2 and 3. Condition in state 2 was higher than in state 3. In contrast, females and juveniles of *P. lineoocellata* appear to be able to compensate reduced prey availability without losing condition by occurring in lower numbers in degraded habitats. This is supported by a study on Sand Dune Lizard (*Acanthodactylus longipes*) where body mass differed not between degraded and non-degraded habitats (Attum and Eason 2006) Then again other studies on lizards showed that a loss of body condition occurs due to increased predation risk (Martin & Lopez 1999, Pèrez-Trís et al. 2004, Amo et al. 2007) which can not be confirmed by our results.

Second, the loss of vegetation cover and the decline of structural diversity reduce predation cover and can increase predation risk (Kotler et al. 1991, Bentley et al. 2000). Vegetation cover serves as retreat or safe site (Norbury 2001, Wasiolka 2004) for a variety of species. For example, Bock et al. (1990) showed that intact areas of bunch grass played an important role for the lizard *Sceloporus scalaris* by providing refuge from predators. Indeed, the amount of lizard tail losses in our study used as a measure for predation risk was significantly higher in degraded habitats compared to non-degraded habitats. Caudal autotomy occurs widely in lizard species and is often used as an anti predatory mechanism (Fox & McCoy 2000). Caudal autotomy has an immediate benefit in the form of survival (Maginnis 2006) but it also has a negative impact (McConnachie & Whiting 2003), namely the cost of tail regeneration (McConnachie & Whiting 2003) and reduced locomotory performance (Fox & McCoy 2000). The energy an individual has to put into tail regeneration (McConnachie & Whiting 2003) may causes a reduction of individual condition (Fox & McCoy 2000, Maginnis 2006). Impaired locomotion causes a reduction of speed and agility (Punzo 1982, Cooper 2003). This can lead to a more difficult escape from predators in future (Martin & Salvador 1992, Cooper 2003) and hence to an increase in mortality (Downes & Shine 2001). Consequently, in areas with increased predation risk lizards spend more energy on survival, e.g. escaping predators by fleeing (Pérez-Tris et al. 2004, Amo et al. 2007) than in areas with lower predation risk. In non-degraded habitats, females can put more energy into breeding instead of putting energy into fleeing from predators. Both a reduction in prey availability and the consequences of increased predation risk can reduce clutch size.

The high predation risk in degraded habitats affects also the survival rate of *P. lineoocellata*. In degraded habitats the annual survival rate was extremely low (Φ = 0.05), whereas in non-degraded habitats the annual survival rate was high (Φ > 0.38).

We conclude that the extremely low survival rate in combination with low birth rates and increased predation risk in degraded habitats leads to sink subpopulations of *P. lineoocellata.* Thus, the species can not constantly colonise degraded habitats without immigration from a nearby source population. In contrast, non-degraded habitats can possibly serve as source areas, because these habitats are characterised by low predation risk, high survival and birth rate as well as by high abundance of adults and juveniles. Thus, it is likely that in non-degraded habitats reproduction is high enough to compensate for losses within the habitat and to supply surplus individuals. These surplus individual can disperse and immigrate into other habitats where individuals can find more space such as in degraded areas (source-sink). However, it is important to know the critical threshold at which the potential source areas do not suffice to compensate the losses of individuals in sinks. In particular, high risks of extinction are expected for isolated populations of species with low dispersal abilities. Therefore, it is crucial to investigate dispersal abilities of *P. lineoocellata* and combine these results with the analysis of population dynamics to develop conservation recommendation, ensuring the long term survival of the species in a variety of habitats over greater areas.

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General Discussion

All four chapters clearly demonstrate that habitat degradation caused by overgrazing had a severe negative impact upon (i) the reptile community as a whole and (ii) on population parameters of *Pedioplanis l. lineoocellata*. Chapter one showed a significant decline of regional reptile diversity and abundance in degraded habitats. In chapter two I demonstrated that *P. lineoocellata* moves more frequently, spends more time moving and covers larger distances in degraded than in non-degraded habitats. In addition, home range size of the lizard species increases in degraded habitats as shown by chapter three. Finally, chapter four showed the negative impacts of overgrazing on several population parameters of *P. lineoocellata*. Absolute population size of adult and juvenile lizards, survival rate and birth rate are significantly lower in degraded habitats. Furthermore, the predation risk was greatly increased in degraded habitats.

Together the results suggest that the five vegetation states investigated can be classified as either non-degraded (vegetation state 1 and 2) or degraded habitat (vegetation state 3 to 5). As all five vegetation states could be easily assigned to one of the two habitat classes. I expect the same result as in the investigated states in chapter three (vegetation state 1 and 3) and chapter four (vegetation state 1, 2 and 3) for the remaining states that were not investigated.

A combination of a variety of aspects can explain the negative impact of habitat degradation on reptiles. First, as shown by the results of chapter one and two reduced prey availability play a major role. Reduced prey availability negatively affects survival rate, the birth rate and overall abundance. Second, the loss of plant cover and structural diversity leads to a loss of niches and microhabitats as well as reducing opportunities for thermoregulation. Furthermore, a loss of cover and structural diversity is associated with increased predation risk and hence, a decrease in population size. I demonstrated in my preceding discussions (Chapter 3 & 4) that these factors are tightly interlinked. If the food resources of a reptile are depleted (Chapter 1 & 2) then abundance decreases (Chapter 1 & 4) and the species has to spend more time in the open, covering greater distances in search of prey (Chapter 2). If a species spends more time moving and moving over greater distances than it is likely that the home range will increase in size as a result, as demonstrated in Chapter 3. Consequently the species predation risk also increases (Chapter 4).

Whereas the increase in home range size could be viewed as an adaptation to limited food resources it might also be expected to lead to a decrease in population size either directly (Chapter 3 & 4) or indirectly via lower survival rates associated with a high predation risk (Chapter 4).

Conclusions

My thesis contributes substantially to the understanding of the impact of overgrazing and resulting shrub encroachment. Habitat degradation not only influences the reptile community as a whole, but also several aspects of population parameter of single species, which are crucial for the survival of a species.

Furthermore, a major finding of my thesis is that the lizard *P. lineoocellata* can alter its foraging strategy to changes in its habitat despite morphological adaptation for a different foraging strategy. Especially in the light of predicted climatic changes (UNEP-IPCC4-Report 2007) behavioural adaptations can play an important role for species in changing environments. For the southern African sub region climatic change forecast predict more severe living conditions, less rainfall and a rise of the daily average temperature (UNEP-IPCC4-Report 2007) which will negatively affect the environment and its inhabitant species.

For a species to persist in habitats subject to environmental change it is crucial that it be behaviourally flexible, particularly if they are to adapt to more extreme living conditions as predicted under climatic change. Species that are able to adapt and change behaviour, such as *P. lineoocellata* can effectively buffer against such changes in their environment. This gives them an advantage over species that are less behaviourally flexible.

A further finding relevant for conservation and management is that perennial grass cover can be seen as a crucial ecological component of the vegetation in the semi-arid savannah system of the southern Kalahari. If perennial grass cover is reduced to a certain degree reptile diversity will decline and most other aspects of reptile population dynamics will be negatively influenced.

United Nations Environment Programme (2007). IPCC WGI Fourth Assessment Report. www.ipcc.ch/SPM2feb.pdf

Savannah systems are characterised by a mixture of woody vegetation, trees and shrubs and perennial grasses (Skarpe, 1992; Teague and Smit, 1992). These three vegetation components determine the composition and structure of the vegetation and accordingly influence the faunal diversity. The recent focus over the last years was laid onto the role of trees and shrubs for faunal diversity in savannah rangeland (e.g. Belsky 1994; Dean et al. 1999).

Trees are viewed as keystone structures and focal points of animal activity for a variety of species (Wichmann 2002; Tews et al. 2004). Several studies showed the positive effect of scattered trees within the grassland savannah matrix. Trees supply species (mammals, birds and lizards) with shelter, shade and food (e.g. Coe and Coe 1987, Dean et al. 1999, Cooper and Whiting 2000) and act as safe sites, nesting sites, observation posts and foraging sites (Dean et al. 1999, Apps 2000, Wichmann 2002). Hence, trees provide the resources and services that are typically scarce in semi-arid savannas helping to support species diversity.

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This contrasts with a long held negative view on the value of shrubs that is based upon the observation that shrub encroached sites tend to be species poor (e.g. Joubert and Ryan, 1999; Seymour and Dean 1999, Eccard et al. 2000, Meik et al. 2002). However, recent research demonstrates a positive influence of shrub patches on several animal taxa and faunal diversity in general (Blaum et al. 2007a, b, Thiele et al. 2007). Thiele et al. (2007) showed a positive relationship between shrubs and bird (Southern Pied Babbler, *Turdoides bicolor*) abundance within the Molopo Nature Reserve, South Africa while Seymour (2006) showed a general increase in avian diversity with shrub cover in the Kimberley region, South Africa. Moreover, it would seem that intermediate shrub cover can also sustain viable populations in savannah landscapes as has been demonstrated for small carnivores (Blaum et al. 2007a) and two rodent species (Highveld Gerbil, *Tatera brantsii* and Striped Mouse, *Rhabdomys pumilio*) (Blaum et al. 2007b). This latter work highlights the role that shrubs can play in determining faunal diversity via vegetation structure.

Blaum N, Rossmanith E, Popp A, Jeltsch F (2007a) Shrub encroachment affects mammalian carnivore abundance and species richness in semiarid rangelands. Acta Oecologica 31, 86-92

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Thiele T, Blaum N, Jeltsch F (2007) Importance of woody vegetation for foraging site selection in the Southern Pied Babbler (Turdoides bicolor) under two different land use regimes. Journal of Arid Environments in press:

The influence of perennial grasses on faunal diversity did not receive the same attention as the influence of trees and shrubs. In my thesis I didn't explicitly measure the direct effects of perennial grasses but my results strongly imply that it has an important role. If the perennial grass cover is significantly depleted (Vegetation state 3 to 5) my results suggest it will negatively influence reptile diversity and abundance and on several populations parameters of *P. lineoocellata*. As discussed in the preceding chapters perennial grass cover is associated with the highest prey abundance, reptile diversity and reptile abundance. It provides reptiles both a refuge from predators and opportunities to optimise thermoregulation.

The relevance of each of the three vegetation structural elements is different for each taxa and species, respectively. In conclusion, I can state that all three major vegetation structures in the savannah system are important for faunal diversity. Because different faunal species groups are closely linked to particular vegetation structures all three structures can be considered as keystone structures. A mixture of tree, shrub and perennial grass assures a greater variety of resources, niches and habitats needed to sustain maximum faunal diversity. Loss of the crucial vegetation structures would have profound implications for nature conservation and biodiversity management.

Zusammenfassung

Die Vegetationskomposition und –struktur, beispielsweise die unterschiedliche Architektur von Bäumen, Sträuchern, Gräsern und Kräutern, bietet ein großes Spektrum an Habitaten und Nischen, die wiederum hohe Tierdiversität in den Savannensystemen des südlichen Afrikas ermöglichen. Dieses Ökosystem wurde jedoch über Jahrzehnte weltweit durch intensive anthropogene Landnutzung (z.B. Viehwirtschaft oder ‚game-farming') nachhaltig verändert. Dabei wurden die Zusammensetzung, Diversität und Struktur der Vegetation stark verändert. Überweidung in Savannensystemen führt zu einer Degradation des Habitates einhergehend mit dem Verlust von perennierenden Gräsern und krautiger Vegetation. Dieser Verlust führt zu einem Anstieg an vegetationsfreien Bodenflächen. Beides, sowohl der Verlust an perennierenden Gräsern und krautiger Vegetation sowie der Anstieg an vegetationsfreien Flächen führt zu verbesserten Etablierungsbedingungen für Sträucher (z.B. *Rhigozum trichotomum, Acacia mellifera*) und auf lange Sicht zu stark verbuschten Flächen bzw. zu Desertifikation. Derartige Veränderungen hinsichtlich der Komposition, Diversität und Struktur der Vegetation führen zu Habitatdegradation, -fragmentation und -verlust, Die Tierdiversität in Savannen wird hiervon entscheidend beeinflusst. Die Konsequenz: Die strukturelle Diversität wird reduziert und die Umweltbedingungen für die Tierwelt verändern sich. Es wurde gezeigt, dass mit reduzierter struktureller Diversität sich auch die Tierdiversität verringert.

Während der Einfluss von Überweidung auf die Vegetation relativ gut untersucht ist sind Informationen über den Einfluss von Überweidung auf die Tierdiversität, speziell für Reptilien, eher spärlich vorhanden. Zusätzlich ist sehr wenig bekannt zum Einfluss auf die Populationsdynamik (z.B. Verhaltensanpassungen, Raumnutzung, Überlebensrate, Sterberate) einzelner Reptilienarten.

Ziel meiner Doktorarbeit ist es den Einfluss von Überweidung durch kommerzielle Farmnutzung auf die Reptiliengemeinschaft und auf verschiedene Aspekte der Populationsdynamik der Echse *Pedioplanis lineoocellata lineoocellata* zu untersuchen. Hinsichtlich bestimmter Naturschutzmaßnahmen ist es einerseits wichtig zu verstehen welchen Auswirkungen Überweidung auf die gesamte Reptiliengemeinschaft hat. Und zum anderen wie entscheidende Faktoren der

Populationsdynamik beeinflusst werden. Beides führt zu einem besseren Verständnis der Reaktion von Reptilien auf Habitatdegradation zu erlangen.

Meine Studie gliedert sich in vier Bereiche unterteilt. Sie untersucht den Einfluss von Überweidung auf:

1. die Diversität und Abundanz der Reptiliengemeinschaft im Savannengebiet der südlichen Kalahari.
2. die Verhaltensanpassung der Echse *P. lineoocellata*.
3. die Raumnutzung (home range) von *P. lineoocellata.*
4. die absolute Populationsgröße, Überlebensrate, Geburtenrate und das Prädationsrisiko von *P. lineoocellata.*

Die wichtigsten Ergebnisse sind im Folgenden zusammengefasst:

Alle vier Teile meiner Doktorarbeit zeigen eindeutig einen negativen Einfluss der Überweidung und der daraus resultierende Habitatdegradation auf (1) die gesamte Reptiliengemeinschaft und (2) auf einzelne Aspekte der Populationsdynamik von *P. lineoocellata*.

Im Teil 1 wird die signifikante Reduzierung der Reptiliendiversität und Abundanz in degradierten Habitaten beschrieben. Im zweiten Teil wird gezeigt, dass *P. lineoocellata* das Verhalten an die verschlechterten Lebensbedingungen anpassen kann. Die Art bewegt sich sowohl häufiger als auch über einen längeren Zeitraum und legt dabei größere Distanzen zurück. Zusätzlich vergrößerte die Art ihr Revier (home range) (Teil 3). Im abschließenden Teil wird der negative Einfluss von Überweidung auf die Populationsdynamik von *P. lineoocellata* beschrieben: In degradierten Habitaten nimmt die Populationsgröße von adulten und juvenilen Echsen ab, die Überlebens- und Geburtenrate sinken, währen zusätzlich das Prädationsrisiko ansteigt. Verantwortlich hierfür ist zum einen die ebenfalls reduzierte Nahrungsverfügbarkeit (Arthropoden) auf degradierten Flächen. Dies hat zur Folge, dass die Populationsgröße abnimmt und die Fitness der Individuen verringert wird, welches sich durch eine Reduzierung der Überlebens- und Geburtenrate bemerkbar macht. Und zum anderen ist es die Reduzierung der Vegetationsbedeckung und der Rückgang an perennierenden Gräsern welche sich negativ auswirken. Als Konsequenz hiervon gehen Nischen und Mikrohabitate verloren und die Möglichkeiten der Reptilien zur Thermoregulation werden verringert. Ein Verlust an Vegetationsbedeckung und struktureller Diversität hat auch einen Anstieg des

Prädationsrisikos zur Folge, was ebenfalls dazu führt, dass die Populationsdichten der Reptilien abnehmen.

Meine Doktorarbeit leiste hiermit einen wichtigen Beitrag zum besseren Verständnis des Einflusses von Überweidung und der daraus resultierender Verbuschung in Savannengebieten.

Danksagung

Zu allererst möchte ich mich herzlich bei meinem Betreuer Florian Jeltsch bedanken. Er hat es mir ermöglicht in einer der schönsten Landschaften dieser Erde, der Kalahari, zu arbeiten. Vielen herzlichen Dank für die für die tolle Betreuung.
Ich danke auch ganz herzlich meinem Co-Betreuer Joh Henschel, der mir immer mit Rat und Tat zur Seite stand.
Ein weiteres großes, herzliches Dankeschön geht an Niels Blaum, der mich immer unterstützt hat mit Rat und Tat und in zahlreichen Diskussionsrunden zum Entstehen der Arbeit entscheidend beigetragen hat.

Nun zu den Personen die mich in während meiner Feldzeit in der Kalahari unterstützt haben. Vielen Dank den Farmern die mir ermöglichten auf ihren Farmen zu arbeiten. Baie Dankie: N. de Wet, K. du Toit, J.J. Eiman, P.H. Eiman, G. Fourie, D.J. Knoetze, K. Marais, D.G. Mouton, E. Riche, L. Schneider, H. Shoeman, S. Snyders, J. Stadler, W. Steyn and A.W. Strauss. Herzlichen Dank Manda, Nico, Hannetjie, Pietie, Bess, de Koker family, Okkie für ihre herzliche Gastfreundschaft, die mir eine sehr angenehme Zeit in der Kalahari beschert hat und für all die Unterstützung die ihr mir gegeben habt.
Ein besonderes Dankeschön gebührt Jörg und Christiane, die mit mir, die ersten Monate das Haus in the middle of nowhere geteilt haben. Herzlichen Dank für die gesellige Zeit, die Hilfe im Feld und einfach nur für die gemeinsame Zeit.
Ich werde meine Zeit in der Kalahari immer im Herzen tragen.

Schließlich danke ich noch meinen lieben Potsdamer Freunden und Arbeitsgruppenmitgliedern, die mir immer geholfen haben wenn Not am Mann und ich ihren Rat benötigte. Sie haben das Leben in Potsdam verschönert und vereinfacht.
Liebe Arbeitsgruppe, vielen Dank für eure Unterstützung, euren Rat in vielen Fragen und der Durchsicht meiner Manuskripte.

Ich danke euch allen von ganzen Herzen.

Meine Arbeit fand im Rahmen des Projektes BIOTA Southern Africa (01LC0024A9 statt und wurde finanziert durch das Bundesministerium für Bildung und Forschung.

“You never ever know if you never ever go”

Ehrenwörtliche Erklärung

Hiermit erkläre ich, Bernd Wasiolka, dass ich die vorliegende Arbeit selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe.

Potsdam, den 31. Dezember 2007

Bernd Wasiolka