



Small mammal community structure (Rodentia: Muridae) in Punda Maria, Kruger
National Park, South Africa: causes and consequences

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A dissertation submitted to the University of Cape Town, in partial fulfillment of the requirements for
the award of an Honours degree in Botany

October 2008

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Abstract

The population dynamics of small mammal populations in Punda Maria, Kruger National Park, South Africa was investigated with respect to community size and structure, seed predation and dispersal of several trees. Species populations, community structure and habitat attributes were measured at six sites comprising of 3 habitat types (2 sites per habitat); namely *Acacia*-grassland, North-facing and South-facing sloped sites. Seasonal variation was investigated at the *Acacia* sites during late summer (April) and winter months (July). Five habitat attributes were measured; percentages of total cover and herbage, plant litter depth (cm), height of dominant vegetation type measured (m) and edaphic condition were recorded at 15 randomly selected traps per site. Almonds (*Prunus dulcis*), baobabs (*Adansonia digitata*), mopane (*Colophospermum mopane*), and *Acacia tortilis* seeds were used in the predation and dispersal experiment. North- and South-facing sites were dominated by *Aethomys* sp. while *Acacia* sites were dominated by *Mastomys natalensis*. Seed predation was high at the North-facing slopes, with a significant difference in predation on *A. tortilis* seeds. Seed dispersal activity was low; no scatter hoarding was identified; only larder hoarding was observed by *Aethomys* sp. and *M. natalensis* at North-facing sites and *Acacia* sites respectively. Trampling by megaherbivore activity impacted vegetation structure and has negatively affected rodent population and ground activity, particularly at the *Acacia* sites.

Key words: Habitat attributes, small mammals, megaherbivores, vegetation structure, seed predation, seed dispersal

Introduction

Mammal herbivores are referred to as keystone species or ecosystem engineers in African savannas, where their activity impacts community structure, plant biomass and ecological processes (Owen-Smith and Danckwets 1997; Whyte *et al.* 2003; Levick and Rogers 2008). Particular attention has been given to megaherbivores such as elephants (*Loxodonta africana*) and white rhino (*Ceratotherium simum*) in this regard (Owen-Smith 1992). Browsing by elephants has been shown to reduce woody plant density and may lead to the conversion of woodlands and shrublands to grassland (Du Toit *et al.* 2003; Sankaran *et al.* 2005; Levick and Rogers 2008). In mesic savannas, negative responses of woody vegetation increased when elephants occur at high densities (Guldemond and van Aarde 2008). In a similar way, although not necessarily at the same intensity or scale, small mammals, such as rodent species, can also have a significant impact on plant community structure, population dynamics and species diversity (Korn 1987a; Korn and Korn 1989; Miller 1994a; Midgley and Bond 2001; van Deventer and Nel 2006) and thus form an integral part of savanna ecosystems. Small mammals are known to have a great impact on seedling recruitment and the extent of this impact has been documented extensively (Miller 1994a; Miller 1994b; Walters *et al.* 2005).

The fate of plant seeds in an ecosystem is important in determining seedling recruitment. Through selective feeding, seed predation, seed dispersal, and levels of seed hoarding, rodents can have a significant influence on plant recruitment, population dynamics, community structure, and maintenance of species diversity (Humble 1998; Crawley 2000; van Deventer and Nel 2006). In the savanna biome, it has been shown that rodents have a preference for certain seeds, specifically *Acacia* species [Miller (1994a) –preference for *Acacia tortillis* seeds; Walters *et al.* (2005) – preference for *A. karoo* seeds]. Miller (1994a) estimated that rodents not only dispersed seeds, but consumed up to 25% of the annual seed crop of *Acacia* species, markedly impacting of seedling recruitment and establishment (Keesing and Crawford 2001; Walters *et al.* 2005). Midgley and Bond (2001) include mammalian herbivores as a key contributor in demographic hurdles for *Acacia* life cycles. The relative impact of rodents as *Acacia* seed predators depends on rodent population density, number of granivorous rodent species, seed composition in their diet, and seasonal fluctuations in alternative food sources. Removal of seeds is often equaled with predation (Miller 1994a; Miller 1994b). However some rodents bury seeds and therefore it is important to discriminate between removal and granivory, and removal and burial (hoarding). Hoarding behavior in savanna systems is poorly documented, and the only experimental evidence for this behavior was shown by Pettifer and Nel (1976). Their findings suggest that the pouched mouse, *Saccostamus campestris*, and the Namaqua gerbil, *Desmodillus auricularis*, are true larder hoarders while *Gerbilliscus brantsii* (documented as *Tatera brantsii* in that article) does not hoard, but occasionally covers seeds, which might be a primitive form of scatter-hoarding. Midgley *et al.* (2002) provided the first field evidence for scatter-hoarding of nuts in the genus *Leucadendron* (Proteaceae) from the southwestern Cape by *Acomys subspinosus*, where seeds were buried singly, less than 2cm deep and at distances up to 5m from the seed depot. Although literature on the fate of seeds in savanna systems is well documented (Miller 1994a; Walters *et al.* 2005; Campbell and Clarke 2006), the importance of having a preference for seeds (Miller 1994a; Walters *et al.* 2005) can be vital in the dynamics of plant recruitment. The red veld rat *Aethomys chrysophilus* is known to have a preference for *Acacia tortillis* seeds (Skinner and Chimimba 2005) and may impact seedling establishment of this species. Rodents can occupy a range of feeding guilds; most are

omnivorous (eg. *Rhabdomys pumilo*, *Mus minutoides*, *Mastomys natalensis*, *Gerbiliscus leucogaster*) and some are also large consumers of grass seeds (eg. *Acomys spinosissimus*, *Mastomys natalensis*) and herbage (eg. *Aethomys namaquensis*, *Thallomys paedulcus*) (Gliwicz 1987; Skinner and Chimimba 2005). Small mammals are very abundant and widely distributed, and form an important component in nearly all terrestrial ecosystems especially in semi-arid and arid systems. Rodent community structure and species richness has been related to habitat structure and complexity, area, productivity, and predation (see Avenant and Cavallini 2007). Variation in rodent habitats is associated with changes in rodent diversity and community structure, and the ecological disturbance of these habitats is associated with a decrease in rodent species richness. Thus, rodents have been identified as valuable indicators of habitat integrity in grassland habitats (Avenant and Cavallini 2007). The “structural complexity” that habitat provides is of utmost importance in determining which rodent communities occur in particular habitats (Fitzherbert *et al.* 2006; Avenant and Cavallini 2007).

In systems where large mammals are present, such as Kruger National Park, their effect on habitat structure is significant. Activity of large mammals especially in areas where population numbers are known to be high can easily be identified by observers; tree felling or browsing by various animals. Another activity that has not received sufficient attention is trampling by these megaherbivores. A “healthy” grassland with various grass species encompassing a range of heights provides a complex habitat for small mammals, especially rodents, by constructing “rodent highways” which aid ordered movement on the ground. Trampling of grass influences this complexity and severely alters rodent populations (Avenant and Cavallini 2007). However, small mammals are often overlooked in the planning, management and conservation of an area. In addition, in South Africa, the ecological factors that influence the structure of small mammal communities in geographically separate areas, even with similar habitats, have not been investigated sufficiently (van Deventer and Nel 2006). Fitzherbert *et al.* (2006) illustrates that our current understanding of habitat preferences of rodents in Africa is weak despite the many studies that have been conducted in this regard. These studies have been conducted in various different ecosystems, each with different study objectives, methodologies and lengths of study periods (Miller 1994a; Keesing 1998; Caro 2001). More importantly, many studies are concerned with population dynamics and small mammal behaviour (Korn 1987a; Korn and Korn 1989; Ellison *et al.* 1993) and much less attention is given to habitat preference, which ultimately forms the basis of small mammal community structure and population dynamic. Habitat preference is however impacted by herbivory and trampling by large mammals in savanna systems.

Herbivory by large mammals is undoubtedly a key driver shaping ecosystem dynamics and biodiversity in savanna systems, such as in Kruger National Park (Du Toit *et al.* 2003; SANParks Management Plan Policy Framework 2006). Disturbance by megaherbivores has a great impact on vegetation structure and may influence structure. Connell (1978) proposed the intermediate disturbance hypothesis which implies that the highest species diversity is obtained in areas of intermediate levels of disturbance, and it is very possible that this hypothesis is valid in disturbed areas in savanna systems. Large mammals shape not only vegetation dynamics, but also have a negative impact on small vertebrate communities (Keesing and Crawford 2001). Large mammal herbivory that alters structural diversity in woody vegetation results in reduced tree recruitment, an increased grass component, increased fires (see Whyte *et al.* 2003) and has a direct impact on rodents (Ferreira and van Aarde 1999). Keesing (1998) and Goheen *et al.* (2004) suggest that *Acacia* seedling survival was 2-fold higher when large mammals were present in their study area, compared to when large mammals were excluded. One possible explanation for the decrease in *Acacia* seedling survival in the mammal-excluded plots is general increase in vertebrates (rodents), and invertebrates (Davidson 1993; Muñoz and Cavieres 2006), which are responsible for the high predation rates on seeds. Where seed consumption by different sized species is high, selective granivory can affect the composition of the plant community (van Deventer and Nel 2006).

Given the high and often devastating impact on *Acacia sp.* by megaherbivores, the relative importance that rodents may have on tree recruitment in the genus *Acacia* is frequently overlooked. *Acacia* trees play an important role both economically and ecologically in savanna systems (Midgley and Bond 2001). Walters *et al.* (2005) and Wiegand *et al.* (2005) suggested that *Acacias* are essential and major contributors to the woody component of savannas, and form a critical part of a cyclical succession - the transition between grassy and woody dominance which is typical of savanna systems. It is clear that small mammals, especially rodents, play a vital role in driving tree recruitment and establishment (Goheen *et al.* 2004). This impact may vary with intensity, especially in times when population numbers are high, which is often in years of high rainfall (Caro 2002). In light of this information and to better understand rodent communities and their habitat preferences in Punda Maria, Kruger National Park, South Africa, the aim of this study was to address the following questions;

- a) Which small mammal communities are found in the study area and how do they vary seasonally and with vegetation structure
- b) Is there an observable change in species composition, dynamics, and structure between the late summer (April) and the winter (July)?
- c) Do the different rodent species have a different preference for certain tree seeds, specifically for certain *Acacias*?
- d) Are the rodents showing any signs of hoarding behavior (either scatter hoarding or larder hoarding) especially during winter months?

We expect that the impact by megaherbivores in the area on vegetation structure has a negative impact on small mammal population and community structure and that the ecosystem function of rodents are lost in this area as a result.

Methods

Study Area

This study was conducted outside the Punda Maria rest camp in the northern region of Kruger National Park, South Africa. The vegetation of the study area is classified in the Makuleke Sandy bushveld which has variable landscapes including low mountains to irregular plains and hills (Mucina and Rutherford 2006). The northern region of Kruger National Park is strikingly different from the rest of the park as it is mainly dominated by woody Mopane (*Colophospermum mopane*) and Bushwillow (*Combretum*) while the ground layer includes dominant grasses such *Digitaria eriantha*, *Panicum maximum* and *Pogonarthria squarrosa* (Mucina and Rutherford 2006; Levick and Rogers 2008). Six sites were divided into 3 classes (based on either vegetation or aspect) with 2 sampling areas per class; (i) *Acacia*-grassland (-22.6987°S; 31.0347°E and -22.6978°S; 31.0336°E), (ii) North-facing slopes (-22.7074°S; 31.039°E and -22.7049°S; 31.0359°E) and (iii) South-facing slopes (-22.6896°S; 31.0303°E and -22.6893°S; 31.0314°E). The two *Acacia*-grassland sites were dominated by grass species such as *Panicum maximum* and *Heteropogon contortus*, and *Acacia nigrescens* and juvenile (<3m) *A. tortilis* species. The North-facing slopes consisted of mixed tree and grass species. Baobabs (*Adansonia digitata*) were present on the northern slopes. The South-facing slopes also consisted of mixed tree and grass species, containing no baobabs and were mainly dominated by Pod mahogany (*Afzelia quanzensis*), whilst apple leaf trees (*Philenoptera violacea*) were present on the footslopes.

Study Map

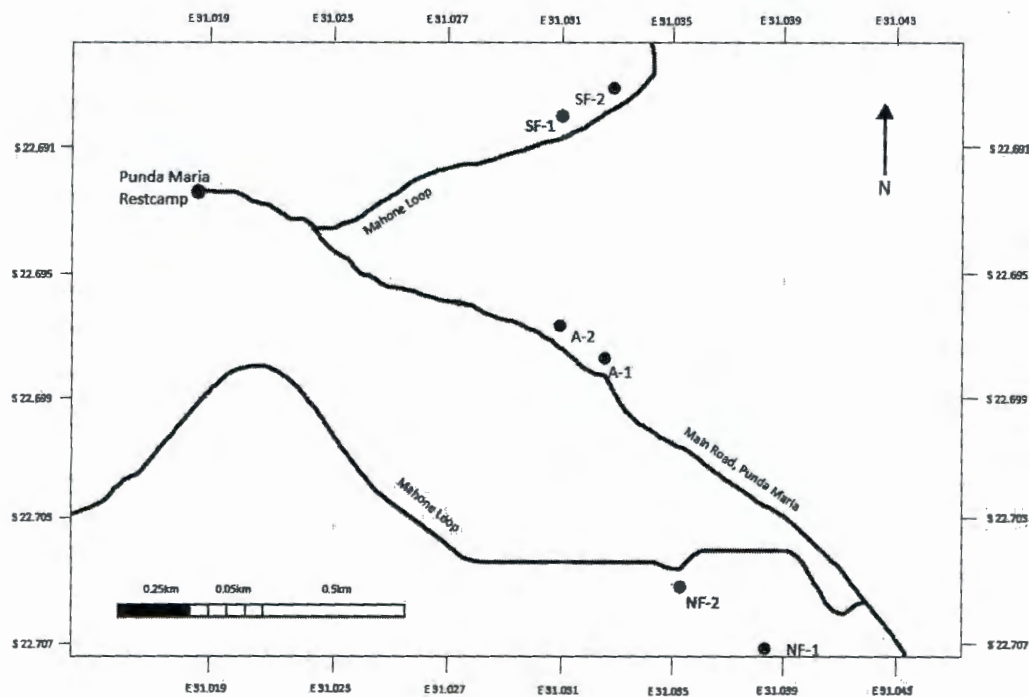


Figure 1. Location of six sampling sites in Punda Maria, Kruger National Park, South Africa - *Acacia*-grassland: A-1 & A-2; North-facing slopes: NF-1 & NF-2 and South-facing slopes SF-1 & SF-2.

Small mammal trapping

Sampling took place on two occasions. The first occasion was part of the Organization for Tropical Studies Program (Fall Semester, 2008) where data were collected at the *Acacia* site for five consecutive nights from 07th to 11th April 2008 (late summer/autumn). The second period of data collection was for eight consecutive days and nights from 23rd July 2008 to 31st July 2008 (winter). Trapping sessions for the second sampling period were divided such that three sites were sampled on the first four nights, and the next three sites on the following four nights.

Small mammals were trapped using aluminum Sherman[®] live traps (230 x 75 x 90mm) with trapping grids comprising of 49 trapping stations arranged in a 7 x 7 configuration with 15m between trapping stations and were distributed in such a way that each trap had sufficient

natural cover whilst keeping the distance between traps as accurate as possible. Trapping sessions lasted for four consecutive days (diurnal) and nights (nocturnal). Each trap was baited with a peanut butter and oats mixture. Rodents were captured and released after being marked with a unique identification number using hair dye subsequent to their weight measured and sex determined.

only in winter.

Data analysis:

Estimates of population densities (individual's ha^{-1}) were based on the minimum number of individuals alive during each trapping session. No immigration, emigration or birth and death were assumed during each trapping session as well as no edge effect due to the short trapping period in April and July. Seasonal variation was only determined at the *Acacia* 1 site following April data, (see Feather-Garner *et al.* 2008 OTS Independent Project). Trap lines at the North-facing 1 and 2 sites and South-facing 1 and 2 sites were strategically placed such that three lines were on the slope and three on the plateau and one line in-between (the transition from slope to flat land). By including the sloped areas for both North and South slopes, the study included a wider range of habitat for small mammals which could have an influence on the savanna system under investigation.

Structural vegetation attributes

Following the methodology of van Deventer and Nel (2006), 15 traps were randomly selected and the following structural vegetation attributes were measured in a 1m^2 quadrat and then averaged per site; Total Cover (%), herbage (% 2m radius), plant litter depth (cm), edaphic composition (sand/gravel/rock), height of dominant vegetation type (m) surrounding the trap (tree, grass or shrub) and shrub (<2m tall) height (m) if present.



Plate 1.1 Acacia sites in April following heavy rains



Plate 1.2 Acacia sites in July (dry season)

The photographs above (Plate 1) were taken at the Acacia A-1 site in April and July. The area experienced a good rainy season between November 2007 and January 2008 (see Figure 2.2) and thus represents a lush tree-grass mixture consisting of several tree species, such as *Acacia nigrescens*, *A. tortilis*, *Combretum apiculatum*, and *Colophospermum mopane* and grass species with seeds such as *Panicum maximum*, *Heteropogon contortus*, and *Urochloa mozambicensis*.

Rodent-Seed preference

Preference tests were carried out on two of the four trapping nights per site. Seeds of four tree species were used in this experiment; almonds (*Prunus dulcis*), baobabs (*Adansonia digitata*), mopane (*Colophospermum mopane*), and *Acacia tortilis*. Seeds of known number (almond n=5, baobab n=5, mopane n=5, *A. tortilis* n=7) were placed on 4 plates per site late in the evening and were checked just after sunrise the next day to avoid activity from animals other than nocturnal rodents, such as tree squirrels (*Paraxerus cepapi*) and baboon (*Papio ursinus*) activity during the day. Plates were placed 30-50m away from the trapping grid (depending on the terrain) to ensure that the trapping grid was not influenced by the presence of the seed plates. Plates were placed under sufficient cover to provide a suitable habitat for rodent activity. Seed preference (seed predation) was quantified and nibbling activity was noted.

Seed dispersal

Seeds were glued onto thread spools which were subsequently glued onto the plates. Thus any seed removal activity could be noted by the direction and distance of the thread. Two of the seeds types (almonds and baobabs) were used in this test as; (i) they were the most preferred, and (ii) the most practical for the gluing process. Four plates were used at each vegetation class, and were placed late in the evening and checked just after sunrise the next day. Plates were placed under sufficient cover to avoid attraction of any other animals, especially larger nocturnal animals.

Data Analysis

Small mammal population estimates were determined using Program MARK V. 5.1. Population estimates were assumed "closed-captures" due to the short trapping period. Shannon-Weiner diversity indices were calculated using PRIMER (Plymouth Routines in Marine Ecological Research) V.6. Species evenness was measured to quantify how equal the communities were using the Shannon-Weiner diversity index. Small mammal community structure and vegetation attributes were analyzed using multivariate techniques (Detrended Correspondence Analysis and Two-way Indicator Species Analysis) to correlate rodent species with habitat attributes in PC-ORD V. 4.25. Differences in seed preferences per site class were measured using Kuskal-Wallis ANOVA by ranks.

Results

Physical attributes of the area

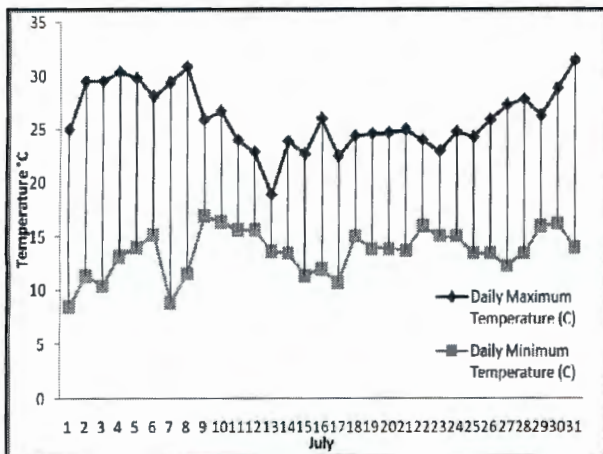


Figure 2.1 July daily minimum and maximum temperatures (°C) in Punda Maria, Kruger National Park

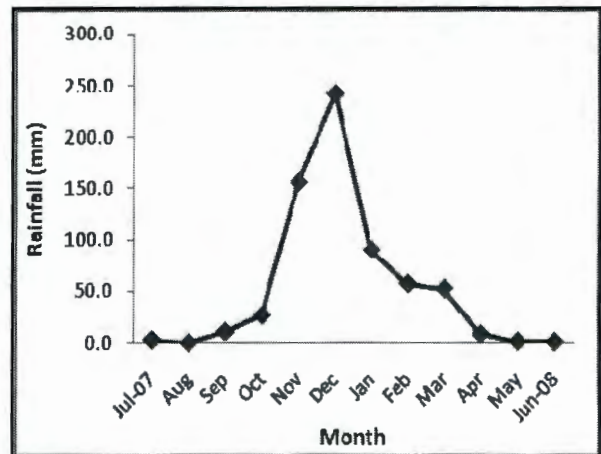


Figure 2.2 Monthly rainfall (mm) from July 2007 to June 2008 in Punda Maria, Kruger National Park

Figures 2.1 and 2.2 represent the temperature and rainfall in Punda Maria, Kruger National Park. The area experienced a good wet season (summer rainfall) that peaks in December represented in Figure 2.2 (KNP rainfall station, Punda Maria).

Small mammal community structure

Table 1 (below) is a summary of estimated rodent population sizes in each site. Trapping success was highest during the April trapping session, with an average of 39.4% over the four nights of trapping. Trapping success was lower in the July trapping session with the lowest success obtained at the Acacia 2 site (11.7%). Only rodents were trapped and tree squirrels, *Paraxerus cepapi*, that were captured during the day were not considered in the analysis of this study. The North facing site population was dominated by *Aethomys sp.* (62.5%) (*Aethomys sp.* could not be indentified to species level due to difficulty in the field, however due to habitat that it occurred; it is most likely *A. chrysophilus*). *Mastomys natalensis* was second most dominant (18.3%) and was found mainly in the two *Acacia* sites. The small mammal population estimate for each site can be obtained in Table 1, with the estimated population sizes for dominant rodent species captured below (Table 2).

Table 1. Small mammal community attributes in three sites; Acacia grassland (Acacia April, July site A-1 and Site A-2), North-Facing slopes (site NF-1 & NF-2) and South Facing slopes (site SF-1 & SF-2) in the northern Kruger National Park, South Africa. Mean (and range values) for number of individuals caught

	Acacia (Apr)	Acacia 1	Acacia 2	North Facing 1	North Facing 2	South Facing 1	South Facing 2
Trapping nights	5	4	4	4	4	4	4
Trap success %	39.4	30.1	11.7	36.2	25	28.1	26.5
No. indivs. caught	197 (26-50)	59 (11-22)	23 (4-7)	71 (16-19)	49 (10-15)	55 (8-17)	52 (8-18)
Density (n/ha)	39.4	14.8	5.8	17.8	12.3	13.8	13
Biomass (g/ha)	48.1	34	28.8	42.8	49.9	51	53.8
Population size (N±SE)	162.26±12.46	88.94±29.03	20±0.5E-05	55.02± 7.24	90.94± 25.48	39.74± 4.66	90.94±25.48
C.I.	(143.54;193.71)	(55.38;180.61)	(20; 20.01)	(46.13;76.77)	(59.91;168.04)	(34.61; 55.02)	(59.91;168.04)
Species richness	6	4	4	3	5	5	3
Species diversity (H')*	1.26	1.09	1.03	0.61	1.04	0.77	0.31
Evenness (E)	0.78	0.79	0.75	0.56	0.65	0.48	0.29

N±SE (lower confidence interval; upper confidence interval)

*Values determined using Shannon-Weiner diversity index

Population sizes with low standard error values indicate a high recapture rate.

Certain sites such as Acacia (Apr), Acacia 1 & 2, North-facing 1 & 2 displays a low variation between communities with their relatively high E value. Species diversity (H') is highest in the Acacia sites, particularly in April, as species richness was highest during this time.

Table 2. Density (n/ha), biomass (g/ha) and species population estimates (N±SE,C.I.) of the dominant species captured at each site. (July study sites are as follow: A-1=Acacia 1, A-2=Acacia 2, NF-1=North-facing 1, NF-2=North-facing 2, SF-1=South-facing 1 and SF-2=South-facing 2)

Species	Site						
	Acacia (Apr)	A 1	A 2	NF 1	NF 2	SF 1	SF 2
<i>Mastomys</i>							
<i>natalensis</i>	(47)	(34)	(13)				
Density (n/ha)	47	32.4	12.4				
Biomass (g/ha)	1537	590.5	249.5				
Population size N±SE (CI)	61.9±7.5 (52.3;83.9)	427.1±412.6 (106.60;2162.8)	*				
<i>Aethomys sp.</i>							
			(4)	(35)	(28)	(28)	(34)
Density (n/ha)			3.8	52.4	26.7	26.7	32.4
Biomass (g/ha)			213.3	1470.5	1421.9	1460	1879.1
Population size			4±0.2E-16	41±4.7	91.8±39.3	32.5±4.3	57.2±9.9
N±SE (CI)			(4;4)	(35.8;56.4)	(49.4;222.5)	(27.94;47.4)	(45.1;87.3)
<i>Gerbilliscus leucogaster</i>							
	(33)	(6)		(15)	(7)		
Density (n/ha)	33	5.7		14.3	6.7		
Biomass (g/ha)	2162.5	306.7		615.2	89.5		
Population size	36±4.35	10.67±4		(38.4±22.5)	11.5±5.7		
N±SE (CI)	(31.3;50.4)	(7.49;34.3)		(19.3;127.4)	(7.7;37.7)		
<i>Saccostomys</i>							
<i>campestris</i>	(29)						
Density (n/ha)	29						
Biomass (g/ha)	1239						
Population size	33.5±5.4						
N±SE (CI)	(27.7;51.6)						

* population estimate extremely high due to lack of recaptures of *M. natalensis* at A2

Species abundances and composition has changed since the April sampling in the *Acacia* 1 site. The *G. leucogaster* population had decreased drastically both in population size (33 animals in April to 10 animals in July) and density (33/ha to 5/ha). One *G. leucogaster* individual from the April trapping session was recaptured in Acacia 1 site in July. No *S. campestris* individuals were found at the Acacia site during the July sampling period, whereas the species was reasonably common during the April survey. Only one *S. campestris* individual was captured at the NF-2 site. *Aethomys sp.* was very abundant, and was the dominant capture species in all the North and South facing slope sites (NF-1, NF-2, SF-1 and SF-2).

Vegetation attributes

Summary of vegetation attributes (mean±SE) obtained for each site are represented in the table below. Sloped sites (North (NF) and South facing (SF)) were generally rocky with a tree-grass mixture. Acacia sites (A-1 and A-2) were dominated by a range of grasses and trees, mentioned in the methods section.

Table 3. A representation of vegetation attributes per site at six study sites in Punda Maria, Kruger National Park

PLDepth=plant litter depth, H. Dominant veg=Height of dominant vegetation type

Attribute	Site					
	A-1	A-2	NF-1	NF-2	SF1	SF-2
Total Cover (%)	26.7±0.2	4±0.01	10±0.2	47.3±0.2	56±0.2	44±0.2
Herbage (%)	68.7±0.2	87.3±0.02	61±0.2	64±0.2	31±0.2	37.4±0.2
PL depth (cm)	1.5±0.04	2.3±0.2	2.8±0.04	2.3±0.2	1.2±0.02	1±0
H. Dominant veg (m)	2.6±0.1	1.1±0.02	2±0.1	2±0.1	1±0.2	2.3±0.1
Edaphic condition	G	G	R/G	R/G	R/G	R/G

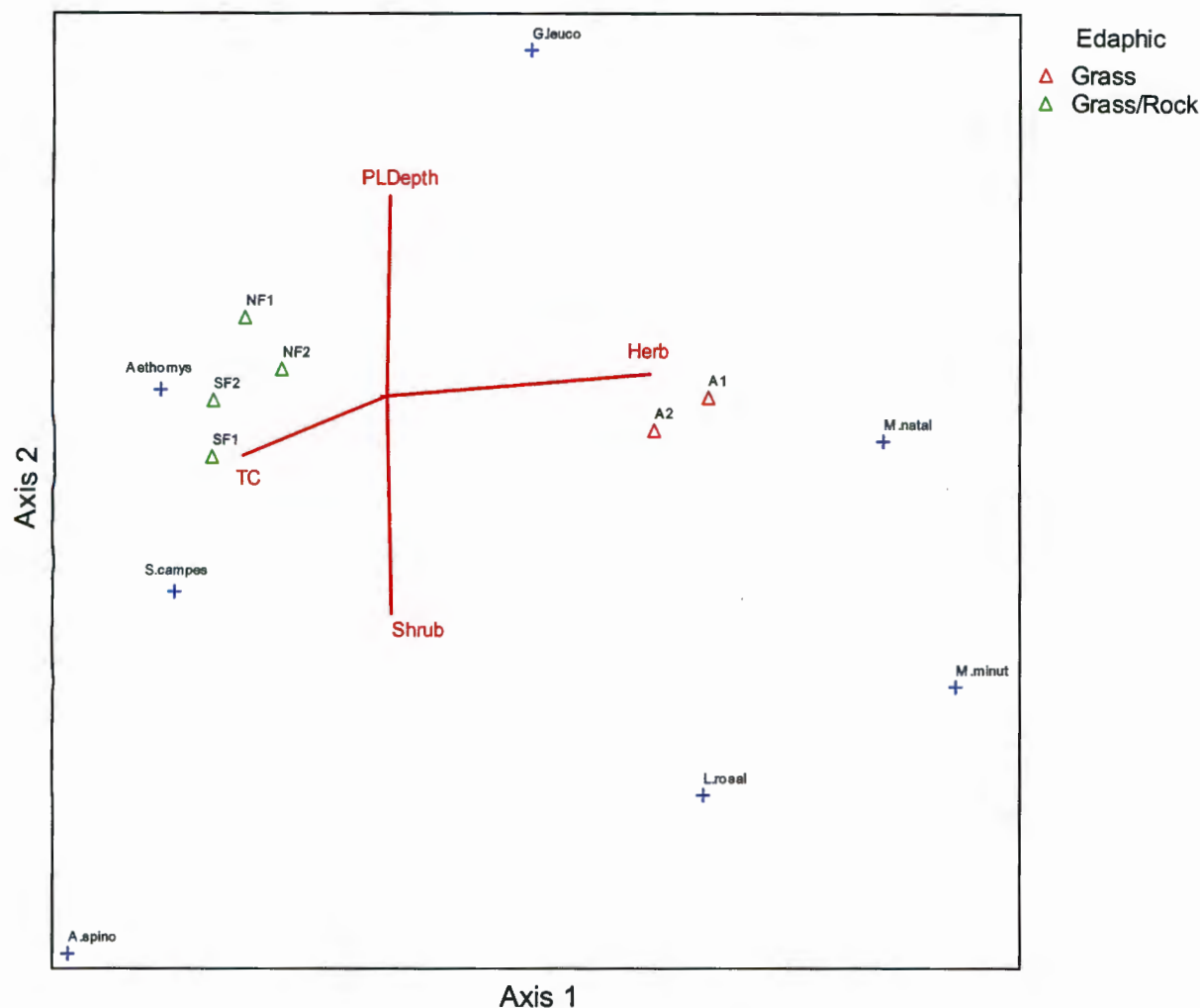


Figure 3. Detrended Correspondence Analysis (DCA) ordination of rodent habitat associations and the vegetation attributes of Punda Maria, Kruger National Park. (PLDepth = Plant Litter depth, HDom = Height of dominant vegetation, TC = Total Cover, Herb=Herbage; A-1=Acacia 1, A-2=Acacia 2, NF-1=North-facing 1,NF-2=North-facing 2, SF1=South-facing 1, SF-2=South-facing 2;G.leuco=*Gerbiliscus leucogaster*, M.natal=*Mastomys natalensis*, M.minut=*Mus minutoides*, L.rosal=*Lemniscomys rosalia*, A.spino=*Acomys spinosissimus*, S.campes=*Saccostomus campestris*, Aethomys=*Aethomys sp.*)

The total variance of the first axis was fairly high (70.2%) with the highest eigenvalues found on axis 1 and 2 (0.478 and 0.057 respectively) (Figure 3). Sites are clearly grouped by edaphic condition and this is reflected in the species captured at these sites. Distances are not a measure of abundance, but position of species associated with sites is an indication of where the species was most abundant. *Aethomys sp.* and *Saccostomus campestris* were mainly found at the sloped sites (NF-1, NF-2, SF1, SF-2) with *Mastomys natalensis* dominant at the grassy

Acacia sites. *Mus minutoides* was only encountered in the *Acacia* 2 site. *Gerbilisicus leucogaster* was encountered at five sites, except site South-facing 2. *Acomys spinosissimus* was encountered on three of the sloped sites, except site South-facing 2. *Lemniscomys rosalia* was found in the *Acacia* 1 site on several occasions, and once in site South-facing 2. The dominant attributes that drive rodent populations appear to be Total cover and Herbage.

Seed Predation

We observed a significant difference in predation on *A. tortilis* seeds [Kruskal-Wallis test: $H(2, N=12) = 8.32, p = 0.02$] (Table 4). *Colospermum mopane* seeds had the lowest predation with no activity observed at both *Acacia* sites, and with very little activity at the North- and South-facing sites. No predatory activity was observed on *A. tortilis* and *C. mopane* seeds at the *Acacia* site. Almonds were highly predated upon at the North- and South-facing sites, but very poorly predated upon at the *Acacia* sites. There was no significant difference in the predation of baobab seeds at each site.

Table 4. Mean (\pm SE) number of seeds not removed or consumed per site ($n=4$ plates per site). Initial number of seeds next to seed type (n)

Site	Seed Type			
	Almond(5)	Baobab(5)	<i>A.tortilis</i> (7)*	<i>C.mopane</i> (5)
<i>Acacia</i>	4.8 \pm 0.1	3.5 \pm 0.6	7	5
North-Facing	0	1.5 \pm 0.6	1.5 \pm 0.8	3 \pm 0.6
South-Facing	0	2 \pm 0.3	0.75 \pm 0.1	3.25 \pm 0.1

* significantly different among sites in K-W test

Seed dispersal

The seed removal experiment did not provide substantial evidence of hoarding behavior. Some seeds were hoarded; at NF-1 site, an *Aethomys sp.* individual removed all seeds directly to its den. Site NF-1 had most activity (predation and removal), while site SF1 had no activity (neither predation nor removal). Site A-1 had activity only on 2 plates that were closely located to a nest. Where removal occurred at site A-1, a seed was taken about 0.5m in an easterly

direction and another 0.2m in a southerly direction. The fate of both seeds was predation overall.

Discussion

Causes of small mammal community structure: biotic vs abiotic factors

In this study, several reasons could explain the observed decrease in population size, species presence and density at the *Acacia* site since April. These include; thermoregulatory adaptations (Ellisson *et al.* 1993) food availability (Gliwicz 1987), predation of rodents (Yarnell *et al.* 2007), and trampling and grazing of vegetation by megaherbivores (Avenant and Cavallini 2007). However the *Acacia* sites had the highest species diversity overall (Table 1). According to Connell (1978) the intermediate disturbance hypothesis might explain the slightly higher species diversity indices (Table 1) obtained for the *Acacia* sites during April and July. High diversity is a consequence of continually changing conditions (Connell 1978). Though disturbance was not measured, it was identified where obvious (eg. Tree felling) and species presence noted by spoor presence (Scholtz and Keith 2008 unpublished data).

Mastomys natalensis is known to tolerate a range of habitats (Skinner and Chimimba 2005) and its population numbers remained relatively stable since the April trapping session (Table 2). This might be due to the wide habitat tolerance that this species is known to have (Skinner and Chimimba 2005). Most of the *M. natalensis* individuals trapped at the A-1 and A-2 site were localized in the trapping grid where the tall grass persists (pers. obs). The A-2 site capture rates were very low and recapture rate very high and indicates a small rodent population size at the study site (Table 1). As suggested by Avenant and Cavallini (2007), an observed lack in grass structure and complexity was evident at this site, allowing movement to be very difficult (Avenant and Cavallini 2007). The reason for this is most likely the effect of large mammals in that particular area. We noticed a high presence of spoor at this site which indicates megaherbivore activity and high grazing activity is known to negatively affect rodent abundance (Yarnell *et al.* 2007). In a similar study, Ferreira and van Aarde (2000) found that “intermediate”

levels of disturbance maintained rodent species diversity, with definite patterns of species turnover evident. *M. natalensis* dominated recently disturbed sites, with *S. campestris* or *A. chrysophilus* more dominant in less disturbed more “stable” sites (Ferreira and van Aarde 2000). The results from this study showed us that *M. natalensis* was dominant in both *Acacia* sites, which had the least total cover (Table 3), and a high presence of *Aethomys* sp. captured in the July sampling period. *Aethomys* sp. dominated captures at the sloped sites during July and indicates a large population of this species in the study area, as they were also captured at the *Acacia* sites. Impact of vegetation (trampling) on rodent trapping success was greatest in the A-2 site, which had substantially lower total cover than the A-1 site (Table 3). Several of the traps in this trampled region at A-2 had no trap success (see Appendix). In general, our results indicate that sites with the highest percentage total cover, maintains the highest small mammal population sizes. Another aspect influencing vegetation cover and composition is abiotic factors; and as the results from this study has shown, vegetation directly impacts small mammal populations.

Abiotic factors such as climate, soil, temperature and rainfall (bottom-up drivers) influence vegetation structure in a similar manner as fire and herbivory (top-down drivers), and as such cannot be treated separately (Du Toit *et al.* 2003). This study indicates that sites with a grass-rock mixture were dominated by *Aethomys* sp. (Figure 3). It is possible that the majority of these individuals were *Aethomys chrysophilus* based on the habitat characteristics in which these species was captured and body mass (Table 2). *Acomys spinosissimus* was found on several occasions at the NF-2, SF1 and SF-2 sites which have a relatively high presence of rocky substrate (Figure 3) and was not encountered at the *Acacia* sites at all. This indicates a strong habitat preference. *A. spinosissimus* is known to be found among rocky outcrops (Skinner and Chimimba 2005). The lack of *Saccostomus campestris* individuals encountered during July can be attributed to be these individuals being in torpor during the winter period (Lovegrove and Raman 1998). Torpor is a thermoregulatory mechanism that conserves energy and is known to be induced by food and water deprivation (Perrin and Richardson 2003). *Mastomys natalensis* populations appeared not to be affected by the temperature. Similarly, *Lemniscomys rosalia*

was encountered on several occasions on the *Acacia* 1 site and only once on the South-facing 2 site. *L. rosalia* was the only diurnal species captured during the July trapping session, in addition to tree squirrels. This species seems to have a habitat preference which agrees with literature (Skinner and Chimimba 2005) and might indicate a localized community succession through seasonality (Yarnell *et al.* 2007) as it was not encountered during the April trapping period.

Many small mammal communities, not just rodents, are influenced by vegetation structure, composition and biomass (Ferreira and Van Aarde 1999; Yarnell *et al.* 2007). The ordination map suggests that total cover (TC) and herbage (Herb) is strongly associated with presence or absence of a particular rodent species (Figure 3, Table 2). Therefore, the structural complexity that grass or a fallen tree provides is essential for the persistence of rodent communities. Figure 3 shows that the vegetation attributes at each site determine rodent species presence. Rodent “runways” (which were more evident at the *Acacia* sites-pers. obs.) were identified wherever long grass was present, and are an indication of ground activity. The structure of the dominant grass species present, such as *Panicum maximum*, has a very narrow base and a multi-branched, open panicle with loose flexuous branches as it reaches a maximum height of 2m (van Oudtshoorn 1992). This habitat structure created by tall grasses is vital in rodent communities (Avenant and Cavallini 2007). This was noted in the Mopane region of the A-1 site, where no rodents were caught due to a lack of ground cover/tall grass. Our results suggest that habitat stability regulates species presence.

In summary, as rodents are good indicators of habitat integrity (Avenant and Cavallini 2007), our sloped sites appear to be “more stable” compared to the *Acacia* sites, indicated by the dominance of *Aethomys sp.* (c.f. *A. chrysophilus*) which agrees with Ferreira and Van Aarde (2000). Both *Acacia* sites were highly disturbed by large mammals and were dominated by *M. natalensis*. Though disturbance was not measured, we propose that the difference in disturbance levels at each site might be linked to accessibility to animals, as sloped sites are harder to access. However, animal activity was noted on these slopes (presence of spoor) although less frequently than on the non-sloped areas (pers. obs.).

Consequences of rodent community structure; seed predation and seed dispersal

Seed predation was evident at the North- and South-facing sites, while the *Acacia* sites had poor seed predatory activity. This could be linked to the species feeding guilds that were present (graminivorous and seed-eating) and the general low population size at the *Acacia* sites, particularly A-2 (Table 1). The dominant species at the A-2 site was *M. natalensis*, which is known to have a preferred diet of insects, followed by fruit and then green plant material (Taylor 1998). *Gerbiliscus sp.*, however, is known to eat equal amounts of insects, seeds and herbage and was present at both *Acacia* sites but was rarely captured at *Acacia* site 2 (Table 2). Though the amount of food available (insects) was very low in dry season (July) (few insects in pitfall traps; Scholtz and Keith 2008, unpublished data), the low seed predation at the *Acacia* sites is an indication of low rodent activity as a consequence of trampling by megaherbivores which reduce structural complexity of the site.

Almonds were most preferred at every site, except the *Acacia* sites (Table 4). Baobabs were predated upon readily at the North- and South-facing sites, although there was no statistical difference between sites. It is possible that rodents may affect seedling establishment of this tree species. Predation on *Acacia tortilis*, however, was significantly different among sites, with NF-1 site having the highest predation (Table 4). This result, in conjunction with the high numbers of *Aethomys sp.* and the preference for *A. tortilis* at this site, suggest that rodents may substantially influence seedling establishment of this tree species.

In summary, rodents, particularly *Aethomys sp.*, may have a significant impact on *Acacia tortilis* seedling establishment in the area. Rodent population sizes are considerably higher in the northern region of the park compared to the southern end of the Park for reasons unknown (G. Ellis pers. comm.). This might be linked to rainfall, frequency of fires, and impacts of large herbivores (Yarnell *et al.* 2007; Guldmond and van Aarde 2008). The site at which *A. tortilis* seeds were highly predated upon had few-to-none *A. tortilis* trees in the general area (one fallen over *A. tortilis* was identified at the site). This might reflect the intense predation

pressure by small and large mammals that is experienced by this tree species in that area and supports suggestion of Miller (1994a) which provided similar results where rodents preferred *A. tortilis* seeds. As suggested by Miller (1994a) and Ferreira and van Aarde (2000) as well as the results of this study, the determinants of abundance and distribution of savanna rodents, particularly those that are known to prefer certain tree seeds, may directly influence patterns of plant establishment (Miller 1994a; Ferreira and van Aarde 2000).

Seed dispersal

Seed removal occurred at all sites; however, at all sites burial was not the fate of the seeds. Many seeds were taken away from the plate and then predated upon with the distances that seeds were taken not exceeding 1m from the plate. Often the seeds were removed from the plate to an area that provided more cover. The burials encountered at A-1 and NF-1 were into a small mammal nest (i.e. larder hoarding). The rodent responsible at A-1 was *M. natalensis* and *Aethomys* sp. at NF-1. Our survey plates were placed in close proximity to the two above mentioned species' nests. The nests were only identified after all the spoils (n=7) entered the same hole underground. *A. spinosissimus* is known to be an insectivore in the savanna (Gliwicz 1987). Its relative, *A. subspinosus* found in the Cape fynbos is known to be a scatter hoarder (Midgley *et al.* 2002). From this study, we can conclude that there were no signs of scatter hoarding behavior at any of our study sites.

In conclusion, the results from this study suggest that disturbance by megaherbivores, not only by grazing, but more importantly trampling which reduces vegetation cover has a great negative impact on small mammal populations and influence rodent habitat and feeding ecology. Disturbance in this area, particularly at the *Acacia* sites, may regulate rodent species richness and potentially affect *Acacia* demography (Miller 1994b; Midgely and Bond 2001). Our results agree with previous studies (Ferreira and van Aarde 1996; Ferreira and van Aarde 2002; Avenant and Cavallini 2007) that *M. natalensis* dominates in disturbed habitats with low vegetation cover. The high population of *M. natalensis* in relation to seed predation and

dispersal is insignificant, as the areas with low vegetation cover had the least seed predatory/dispersal activity. The seasonally variable rodent populations in conjunction with seed predation that was clearly evident at our North- and South-facing sites may influence tree seedling recruitment, especially for *A. tortilis* seedling establishment. The succession of rodent communities observed in this area is very valuable in understanding rodent population dynamics in the area. Many of the species captured during April were not found during July. It may seem that the species community shift may have adverse effects on certain tree species seedling establishment such as *A. tortilis* during particular times of the year when *Aethomys sp.* populations are high. Rodents are valuable indicators of habitat integrity (Avenant and Cavallini 2007) and will provide substantial information of rodent-habitat association and feeding ecology of small mammals in the area. The need for annual rodent trapping should be highly important in this area of the park, in an attempt to increase the understanding of these large rodent populations that thrive in this region of the park.

Acknowledgements

Special thanks to SANParks for giving me the opportunity to work in one of the most beautiful places on earth. The Organization for Tropical Studies, South Africa for the use of their equipment and funding transport within the park. Jeremy Midgley for guidance and more importantly funding this project. Mark Keith for the continuous hard work in the field and the guidance. My honours class for the support and keeping the sanity at times. The OTS group (Fall Semester 2008), particularly Sofia Solano-Fernandez and Sophie Feather-Garner with whom I worked closely, Graeme Ellis and Karen Vickers for help with data collection in April.

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Appendix

Trap #	A HDomV	A TotCov	# Trapped	AA HDomV	AA TotCov	# Trapped	NF HDomV	NF TotCov	# Trapped	NE HDomV	NE TotCov	# Trapped	SF HDomV	SF TotCov	# Trapped	SN HDomV	SN TotCov	# Trapped
1-1	5	5	2	3	4	3	3	4	0	2	5	1	2	3	0	4	4	1
1-2	2	3	5	1	3	0	3	4	2	2	3	0	4	3	0	2	4	1
1-3	4	4	1	5	2	0	3	0	0	1	3	0	4	3	1	3	4	0
1-4	4	4	0	1	2	1	3	0	0	2	2	0	2	2	2	2	4	0
1-5	3	0	2	1	1	0	3	5	0	2	3	1	3	3	0	1	4	0
1-6	4	4	1	1	4	0	4	0	0	6	4	0	3	2	0	2	5	0
1-7	5	3	0	2	4	0	3	4	0	4	2	0	5	2	0	3	3	0
2-1	3	5	4	4	0	2	3	4	0	2	5	0	4	2	0	2	3	1
2-2	2	3	3	2	4	0	3	0	1	4	5	1	4	2	0	4	4	1
2-3	4	4	0	2	0	0	3	0	0	2	1	1	4	4	0	3	4	0
2-4	1	3	1	1	0	0	3	3	3	3	3	0	7	3	0	3	1	0
2-5	2	5	0	1	1	0	4	4	0	2	2	0	4	2	0	3	2	0
2-6	4	4	0	1	2	1	2	0	0	3	3	0	3	2	1	4	1	0
2-7	3	5	0	1	3	0	3	4	1	3	3	0	3	2	1	5	1	1
3-1	2	1	5	4	0	0	3	5	0	2	1	0	4	2	1	3	2	0
3-2	4	4	3	2	0	0	3	4	1	2	1	0	2	1	2	4	1	0
3-3	3	4	2	3	0	0	3	5	0	2	1	0	4	2	2	3	2	0
3-4	4	4	2	3	0	0	3	3	0	4	4	1	3	4	0	1	2	0
3-5	2	1	0	1	1	1	3	3	0	3	3	1	3	4	1	4	2	1
3-6	4	4	0	2	2	1	4	0	0	4	3	1	4	4	2	3	2	0
3-7	3	4	0	1	3	1	2	0	0	4	3	0	2	3	0	4	4	0
4-1	4	4	3	4	1	0	5	3	2	2	3	0	3	2	1	4	1	1
4-2	4	3	5	3	1	0	4	2	3	4	3	2	4	3	1	4	1	0
4-3	2	4	4	1	3	0	4	0	1	4	1	1	4	3	0	5	3	1
4-4	2	1	3	2	3	0	5	2	2	3	1	1	4	2	0	4	4	0
4-5	3	5	0	1	2	0	8	1	1	3	3	2	2	4	0	2	2	1
4-6	4	1	1	1	1	1	5	2	2	4	3	3	3	3	1	3	2	0

4-7	2	2	0	1	2	2	4	3	2	5	3	0	3	3	1	3	3	2
5-1	2	4	0	3	0	0	3	3	4	4	2	3	1	3	2	3	2	3
5-2	4	5	1	4	1	0	4	2	2	2	2	0	4	4	0	4	2	1
5-3	5	2	1	1	4	0	3	0	1	4	4	2	2	2	1	5	3	2
5-4	3	3	0	2	2	0	8	1	1	5	2	0	2	4	1	6	4	1
5-5	4	5	0	1	1	0	4	1	4	7	1	1	2	3	2	4	2	0
5-6	5	1	0	1	2	0	3	3	1	2	1	4	5	3	1	3	2	0
5-7	8	2	0	5	2	0	3	4	2	4	3	0	5	2	0	4	3	2
6-1	7	2	0	4	0	4	4	1	2	5	4	2	2	2	1	2	2	2
6-2	4	2	1	3	0	0	3	3	0	1	2	0	6	3	1	3	3	0
6-3	2	3	0	1	4	0	3	1	3	6	2	0	3	2	1	3	4	2
6-4	2	1	0	1	3	0	7	2	0	4	2	1	6	1	1	2	4	1
6-5	3	4	1	1	3	0	7	3	0	5	1	0	2	4	2	3	3	0
6-6	4	1	0	2	3	1	3	1	1	4	1	1	4	4	1	2	2	2
6-7	4	1	0	1	1	0	7	1	1	4	1	2	3	1	2	2	2	3
7-1	8	3	0	2	0	2	3	1	0	6	1	1	3	3	1	3	2	1
7-2	7	3	0	4	0	2	3	4	1	5	1	2	3	3	1	2	3	1
7-3	3	1	0	1	1	0	4	2	3	5	1	2	3	2	0	2	1	1
7-4	7	1	0	1	1	0	4	2	1	4	2	2	1	1	0	2	2	0
7-5	4	1	0	2	4	1	4	2	0	8	2	1	2	1	0	2	2	0
7-6	3	1	0	1	5	0	4	1	2	2	1	1	4	2	1	2	2	0
7-7	3	1	0	2	4	0	3	1	2	2	3	1	4	3	0	2	3	1

Table 1. Data showing trap success of all traps at all sites. Height of dominant vegetation (Hdom) given as well as Total cover (Totcov) for all traps.