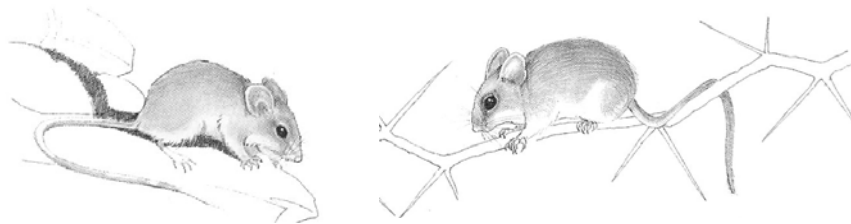# The impact of habitat structures on some small rodents in the Kalahari Thornveld (South Africa)

Dissertation

zur

Erlangung des Doktorgrades
der Naturwissenschaften
(Dr. rer. nat.)

dem Fachbereich Biologie
der
Philipps-Universität Marburg
vorgelegt
von

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aus Saalfeld (Saale)

30. März 2004

I. Contents

1. Erklärung zu eigenen Beiträgen und Veröffentlichungen

Laut Promotionsordnung der Philipps-Universität Marburg vom 29. November 1989 müssen die jeweiligen Anteile des Doktoranden an den Forschungsarbeiten deutlich abgrenzbar sein.

Die vorgelegte Dissertation besteht aus einer Sammlung von Manuskripten, die sich in unterschiedlichen Stadien der Veröffentlichung befinden. Nachfolgend werden die jeweiligen Beiträge des Verfassers an den vorgelegten Manuskripten näher bezeichnet.

Kapitel 4.: Heterogeneity and predictability of habitats and the small rodent community in the Thornveld savannah, South Africa.

- Planung und Durchführung der Feldarbeit.
- Auswertung und Erstellen des Manuskriptes.
- Das vorliegende Manuskript soll bei *Journal of Arid Environments* eingereicht werden.

Kapitel 5.: Nesting sites and nest density of *Aethomys namaquensis* (Rodentia, Muridae) in the Thornveld savannah of South Africa.

- Planung und Durchführung der Feldarbeit.
- Auswertung und Verfassen des Manuskriptes zusammen mit Prof. Brandl.
- Das Manuskript wurde bei *Mammalian Biology* eingereicht und befindet sich im Druck. Die vorliegende Version entspricht dem eingereichten Manuskript.

Kapitel 6.: Space use, circadian activity pattern, and mating system of the nocturnal Black Tailed Tree Rat *Thallomys nigricauda*.

- Planung und Durchführung der Feldarbeit und Auswertung zusammen mit J.A. Eccard.
- Beteiligung am Verfassen des Manuskriptes als Koautor.
- Das Manuskript ist im *Journal of Mammalogy* (vol. 85, issue 3, p. 440-445) erschienen. Die hier vorgelegte Version beinhaltet bereits die Vorschläge und Hinweise der Gutachter, stellt jedoch nicht die endgültige Druckversion dar.

Kapitel 7.: Notes on the ecology of the Black Tailed Tree Rat (*Thallomys nigricauda*).

- Planung und Durchführung der Feldarbeiten. Die Fang-Wiederfangstudie wurde durch J. Steinhauser unter Anleitung des Verfassers durchgeführt. Die Auswertungen zur Populationsgröße und Mortalität wurden durch J. Steinhauser vorgenommen.
- Auswertung und Erstellen des Manuskriptes zusammen mit J. Steinhauser und Prof. Brandl.
- Das Manuskript soll bei *African Zoology* eingereicht werden.

Kapitel 8.: Diet of the arboreal Black Tailed Tree Rat (*Thallomys nigricauda*).

- Planung und Durchführung der Feldarbeiten und der Probenaufbereitung (Präparation, Erstellen eines Bestimmungs-schlüssels, Festlegung der Auswertungsroutine).
- Verfassen des Manuskriptes zusammen mit Prof. Brandl.
- Das Manuskript wurde bei *African Journal of Ecology* eingereicht. Das vorliegende Manuskript entspricht der eingereichten Fassung.

Kapitel 9.: Vegetation structure and the abundance of the Black Tailed Tree Rat *Thallomys nigricauda* at the Thornveld savannah (South Africa).

- Planung und Durchführung der Feldarbeit.
- Auswertung der Daten und Erstellen des Manuskriptes zusammen mit Prof. Brandl.
- Das Manuskript soll demnächst bei einer (tier-)ökologisch orientierten Zeitschrift eingereicht werden.

2. Zusammenfassung

Die Stabilität des Ökosystems Savanne wird wesentlich durch die Häufigkeit und Intensität von Bränden sowie durch die Wirkung grasender und Gehölze verbeißender Tiere bestimmt. Durch die zunehmende Nutzung von semiariden Savannen für die Zucht von Rindern und anderen Haustieren steigt der Einfluß der Beweidung (grasende Tiere) während gleichzeitig die Wirkungen von Gehölz verbeißenden (viele Antilopen, Giraffen) abnimmt. Feuer werden aktiv durch die Farmer bekämpft. In der Summe führt dies zu einer Zunahme von dornigen Sträuchern bei gleichzeitiger Reduktion des Grases. In den Bereichen um Wasserstellen, Siedlungen und Wechseln wird die ausdauernde Vegetation vernichtet und offener Sandboden liegt vor. In Jahren mit ausreichenden Niederschlägen werden diese gestörten Flächen oft von ungenießbaren, einjährigen Pflanzen bedeckt.

Vor diesem Hintergrund wurden der Einfluß von zunehmend verbuschten sowie offener, mit einjährigen Pflanzen bedeckter Flächen auf die kleinen Nagetiere einer semiariden Savanne in der Republik Südafrika untersucht. Dabei stellt die vorliegende Arbeit grundlegende Informationen zur Kleinsäugergemeinschaft des Gebietes bereit. Um einen möglichst breiten Bereich von möglichen Reaktionen der Arten und Gemeinschaften zu erhalten, wurden sowohl terrestrische, als auch arborikole kleine Nager untersucht. Mit dem Begriff „Kleinsäuger" werden nachfolgend nur die kleinen Nagetiere bezeichnet.

Die Grundhypothesen dieser Arbeit sind:

i) Die zunehmende Dichte von Büschen reduziert die Grasbedeckung und wirkt sich negativ auf die terrestrische (zumeist grani- / herbivore) Kleinsäugergemeinschaften aus.

ii) Arborikole, folivore Nager, hier speziell die Akazienratte (*Thallomys nigricauda*), reagiert positiv auf die zunehmende Vernetzung des Lebensraumes und ein potentiell verbessertes Nahrungsangebot.

iii) Auf gestörten Flächen ist die Diversität der Kleinsäuger geringer als auf Flächen mit mehrjähriger Pflanzenbedeckung.

4

Der Inhalt der einzelnen Kapitel dieser Dissertation wird nachfolgend kurz zusammengefaßt:

Kapitel 4:

In diesem Kapitel wird die generelle Zusammensetzung der Kleinsäugergemeinschaft und deren Verteilung entlang eines angenommenen Heterogenitätsgradienten im Untersuchungsgebiet näher betrachtet. Dabei wurden gezielt die im Sommer 2002 mit einjährigen (annuellen) Pflanzen bedeckten stark gestörten Flächen berücksichtigt. Hinsichtlich ihrer Bedeckung hängen diese Flächen völlig vom Regen im jeweiligen Jahr ab und sind somit für Kleinsäuger „unvorhersehbare" Habitate. Der Fang erfolgte mit Lebendfallen, die in 4x5 bzw. 6x6 Feldern (mit jeweils 10 m Abstand zwischen den Fallen) angeordnet wurden. Gefangen wurde jeweils eine Nacht auf 26 Flächen, die vier Habitate repräsentierten (dominierend annuelles Gras; perennierendes Gras; gemischte Flächen mit < 30 % Gras und gemischte Flächen mit ≥ 30% Gras).

In 751 Fangnächten wurden 85 Individuen aus sieben Arten gefangen. Das entspricht rund 50% des potentiellen lokalen Artenpools. Zwei Arten (*Tatera brantsii*; Gerbil) und *Elephantulus intufi*; Elefantenspitzmaus) waren nur mit einem Individuum vertreten und wurden deshalb von der Analyse ausgeschlossen. Für die drei häufigsten Arten *Tatera leucogaster*, *Saccostomus campestris* und *Aethomys namaquensis* wurden weite, sich überlappende Nischen ermittelt. Sowohl die Diversität der unterschiedenen Strukturelemente, als auch das Vorhandensein von ausdauernden Gräsern waren positiv mit den Artenzahlen, den relativen Abundanzen und der Diversität der Artengemeinschaften korreliert. Die relativen Abundanzen der einzelnen Arten waren ebenfalls positiv mit ausdauerndem Gras und negativ mit der annuellen Vegetation auf gestörten Flächen korreliert. Die Ausnahme war der Kurzschwanz-Gerbil (*Desmodillus auricularis*), der offene Flächen bevorzugt. Gestörte Flächen zeigten geringere totale Abundanzen und die geringste Artenzahl. Sie werden deshalb, zusammen mit ihrer unvorhersehbaren Verfügbarkeit als langfristig ungünstige Habitate angesehen.

Kapitel 5:

Hier wurden die Habitatansprüche der terrestrischen und Kolonien bildenden *Aethomys namaquensis* (Namaqua Stein Maus) im Untersuchungsgebiet analysiert. Die Art kommt im ganzen südlichen Afrika vor und scheint deshalb in der Lage zu sein, sich mit einer breiten Palette von strukturellen Gegebenheiten zu arrangieren. Andererseits werden die Nester meist mit großen Mengen Gras bedeckt, was eine Bindung an ausreichende und ausdauernde Grasbedeckungen impliziert. Im Untersuchungsgebiet wurden Daten von 92 Nester von *A. namaquensis* sowie deren assoziierten Strukturen erhoben. Zusätzlich wurden auf 14 ausgewählten Flächen die wesentlichen Habitatparameter abgeleitet. Alle gefundenen Nester waren mit Holzstrukturen, meist mit liegendem Totholz, assoziiert. Die am Boden errichteten Nester nutzen zumeist liegende große Bäume oder aber den Kronenbereichen von gefällten Büschen von *Boscia albitrunca*. Die Größe der Initialstrukturen stand nicht im Verhältnis zur Größe des darauf errichteten Nestes (ausgedrückt als Volumen der Graskuppel). Nester in stehenden Stümpfen und Bäumen wiesen ein wesentlich geringeres Volumen auf und wurden nur im regenreichen Sommer 2002 gefunden. Die Analyse der Habitate ergab eine signifikant negative Beziehung der Nestdichte (ha^{-1}) zu gestörten Flächen. Durch Nutzung bedingte Vegetationsveränderungen können sowohl negativ (Störungsbereiche) als auch fördernd (Schaffung von Totholz) auf das Vorkommen von *A. namaquensis* wirken.

Kapitel 6:

Die hier vorgestellten Ergebnisse einer Radiotelemetriestudie lieferten die Grundinformationen zum räumlich-zeitlichen Verhalten der Akazienratte (*Thallomys nigricauda*). Während der Fortpflanzungszeit im Sommer 2001 und dem Winter 2001 (keine Reproduktion) wurden 14 adulte Tiere (3 Männchen und 4 Weibchen im Sommer; 2 Männchen und 5 Weibchen im Winter) mit Halsbandsendern ausgestattet. Das Aktivitätsmuster war rein nachtaktiv und bimodal, mit einem Aktivitätshoch sommers kurz nach Sonnenuntergang und einem weiteren Hoch am Morgen. Adulte Männchen waren durchgehend aktiver als säugende Weibchen. Im Winter blieb das Aktivitätshoch nach Sonnenuntergang bestehen, das allgemeine Aktivitätsniveau lag

aber in beiden Geschlechtern niedriger. Die überlappenden Reviergrößen der Männchen während der Fortpflanzungszeit waren wesentlich größer als erwartet (bis 10 ha), während die von säugenden Weibchen auffallend klein waren (bis 0,03 ha). Im Winter nutzten die Männchen kleinere, nicht überlappende Reviere. Weibchen waren auf Flächen von 0,1 bis 0,3 ha aktiv. Neben den Nestbäumen wurden die Büsche *Acacia mellifera* und *A. luederitzii* häufig genutzt. Da die Reviere der Männchen Nester mehrerer Weibchen beinhalten, wird ein polygynes Paarungssystem angenommen. Die in der Literatur beschriebene Bildung von Kolonien oder Familienverbänden konnte nicht bestätigt werden.

Kapitel 7:

Zur Biologie der Akazienratte *Thallomys nigricauda* lagen bislang keine Daten und Freilanduntersuchungen vor. Im Sommer 2002 wurde eine Fang-Wiederfang-Studie auf zwei Untersuchungsflächen durchgeführt. Unter Hinzuziehen von Fangdaten aus 2001 konnten erstmals Aussagen zur Demographie, den sekundären Geschlechterverhältnissen, Populationsdichten und Mortalitätsraten getroffen werden. Es wurden Wachstumskurven für Jungtiere (bis 50 g) abgeschätzt, wodurch der zeitliche Verlauf des Reproduktionsgeschehens nachvollzogen werden konnte. Die ersten Paarungen finden Mitte bis Ende Oktober statt. Aufgrund der jährlichen Verteilung des Regens sollten die letzten Würfe Ende März erfolgen, um den Jungtieren das Erreichen ein ausreichend hohes Gewicht zu ermöglichen, das ein Überleben des Winters begünstigt. Das Einsetzen der potentiellen Geschlechtsreife (Hoden skrotal, Vulva geöffnet) wurde für ein Körpergewicht von rund 40 g bzw. ein Alter von etwa 60 Tagen festgestellt. Verfügbare Literaturangaben sind kritisch zu betrachten, zumal die Schwesterarten *T. nigricauda* und *T. paedulcus* möglicherweise vermischt wurden.

Kapitel 8:

Ausgehend von gelegentlichen Beobachtungen aus dem Kalahari Gemsbok National Park wurde angenommen, daß die Akazienratte *Thallomys nigricauda* unter anderem an Akazien frißt. Im Untersuchungsgebiet wird die Verbuschung durch die Arten *Acacia mellifera* und *A. luederitzii* dominiert. Eine Analyse von Kotproben aus dem Sommer

und dem Winter ergab eine sehr starke Nutzung dieser beiden Pflanzen (95% der identifizierten Fragmente). Diese Präferenz bleibt auch während des Winters erhalten, obwohl dann beide Büsche nur trockenes Laub tragen. Möglicherweise bieten die dornigen Büsche einen sehr guten Schutz vor Beutegreifern. Zudem kann die Akazienratte präformiertes Wasser auch aus trockenem Laub verwerten. Die relative Dominanzen der Futterpflanzen auf den jeweiligen Untersuchungsflächen muß sich nicht in der Nahrung niederschlagen. Wahrscheinlich liegen individuelle Präferenzen vor oder aber die Distanz vom Nest zur nächsten Futterpflanze ist entscheidend. Eine Zunahme der beiden Akazienarten durch Verbuschung verbessert potentiell das Nahrungsangebot für *T. nigricauda*.

Kapitel 9:

In diesem Abschnitt werden die Habitatansprüche der Akazienratte *Thallomys nigricauda* analysiert. Die relativen Abundanzen von *T. nigricauda* wurden mittels Index (Anzahl von Nestern und Kot-Ansammlungen pro Hektar) bewertet. Das Vorkommen von *T. nigricauda* wird durch große, lebende Bäume (> 5 m) und Futterpflanzen (*Acacia mellifera* und *A. luederitzii*, > 1 m) bestimmt. Die meisten Nester befinden sich in lebenden Bäumen (meist *Boscia albitrunca*) sowie toten Bäumen und Stümpfen. Zweignester, wie in der Literatur gelegentlich beschrieben, stellen keine alternative Neststrategie dar. Um als Nestbaum geeignet zu sein, müssen Futterpflanzen in der Nähe vorhanden sein (< 15 m). Säugende Weibchen und ihre Jungen wurden nur in Nestern gefunden, die im Traufbereich des Nestbaumes (patch) oder unmittelbar daneben mindestens eine Futterpflanze (> 1 m) aufwiesen. Die Kombination „großer Baum und Futter" ist im Untersuchungsgebiet nicht häufig. Damit könnte das Vorhandensein von potentiellen Nestbäumen und assoziierten Futterpflanzen limitierend für die Populationen von *T. nigricauda* sein. Für das Vorkommen der Akazienratte sollten mindestens ein großer Baum und etwa zehn Futterpflanzen pro Hektar vorhanden sein. Die Verbuschung verbessert die Lebensbedingungen der Akazienratte.

3. Introduction

3.1 General introduction

Savannahs

Grassland and savannah ecosystems comprise about 10% of the land surface and can be found around the world (Delany and Happold, 1979; Jeltsch et al., 2000). The characteristically appearance, namely the scattered distribution of trees in a grassy matrix makes this ecosystem easy recognisable. It occurs over a wide range of precipitation, topography and climate. At a local scale, savannah types have been distinguished according to special features within the vegetation composition (e.g. for Africa by Keay, 1959; Acocks, 1988). An important character of this ecosystem is the seasonality of rain and consequently a periodic pattern of primary productivity (Delany and Happold, 1979). Species living there are adapted regarding their reproduction cycles to the limited time span of sufficient precipitation for flowering in plants and for raising offspring in animals. Severe problems may arise as the variability of rainfall among years is considerably high (fig. 1) and decisions regarding reproduction have to be made before the animals "know" the progress of rainfall within the particular year.
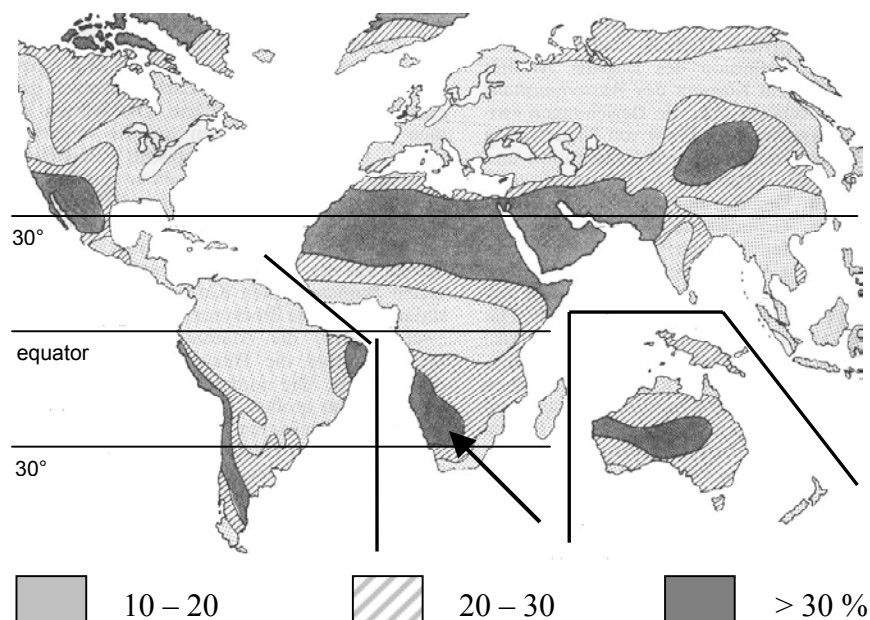
Fig.1 Worldwide distribution of mean annual variation of rainfall (CV in %; after Goudie, 1995). The arrow shows the location of the study area.

Despite the large amount of research on savannah systems for decades, there is still no proven knowledge, why the general assemblage of grasses and trees persists over such a broad range of conditions, without one vegetation type becomes dominating the other (Jeltsch et al., 1996; Jeltsch et al., 2000; van Langevelde et al., 2003). The equilibrium hypothesis discussed in the past claimed grasses and trees having access to water at different soil depths (Walter, 1971). That theory was intuitively, but could explain only for a stable balance of grass and trees. If including additional traits like fire or herbivory, either the "normal" savannah or a dominating shrub-cover without any noteworthy amounts of grass could have developed. Recently, non-equilibrium models have replaced those theories. Savannah-like ecosystems are now considered not to represent a more or less stable state, rather than a system existing between boundaries (Jeltsch et al., 2000; Ludwig et al., 2003; van Langevelde et al., 2003). Buffering mechanisms are discussed, which prevent the ecosystem crossing its boundaries and maintain it. Consequently, grasslands and savannahs are considered to keep their typical appearance throughout a continuous range of structural assemblages. Fire is argued to be a steering factor of savannah persistence as burning removes aboveground grass, and it is damaging and frequently killing small woody plants. Consequently, the amount and spatial distribution of grassy fuel load influences the intensity as well as frequency of fires, preventing the establishment of a dense woody cover. On the other hand, if shrubs have succeeded to establish, they suppress grasses around, forcing a clumped spatial pattern within shrubs and trees (Jeltsch et al., 1996). Another important factor is the strength and type of herbivory. Grazers reduce the amount of grasses, giving woody plants a competitive advantage, whereas browsing animals like giraffes decline the woody cover and give grasses an indirect support (fig. 2).

Human use of semi-arid savannahs does considerably affect the factors fire and herbivory. Fires are actively prevented on farmland, whereas at the same time grazing livestock, mainly cattle, reduce the grass cover. As a consequence, woody plant cover increases, forcing a process called "shrub encroachment" (Ryan and Joubert, 1997; Schultka and Cornelius, 1997). Browsing large ungulates like some antelopes are present at some farmlands, but not in sufficient numbers to compensate the grazing pressure by livestock.

An additional sign of habitat deterioration is the increasing proportion of open ground due to trampling and overgrazing. Especially around water holes, settlements and paths the perennial grass cover has vanished and bare soil occurs (Jeltsch et al., 1997). During

years with a sufficient amount of rain, those areas might become covered with unpalatable annual plants like the Kalahari Sour Grass (*Schmidtia kalahariensis*) or Goosefoot (*Chenopodium album*).
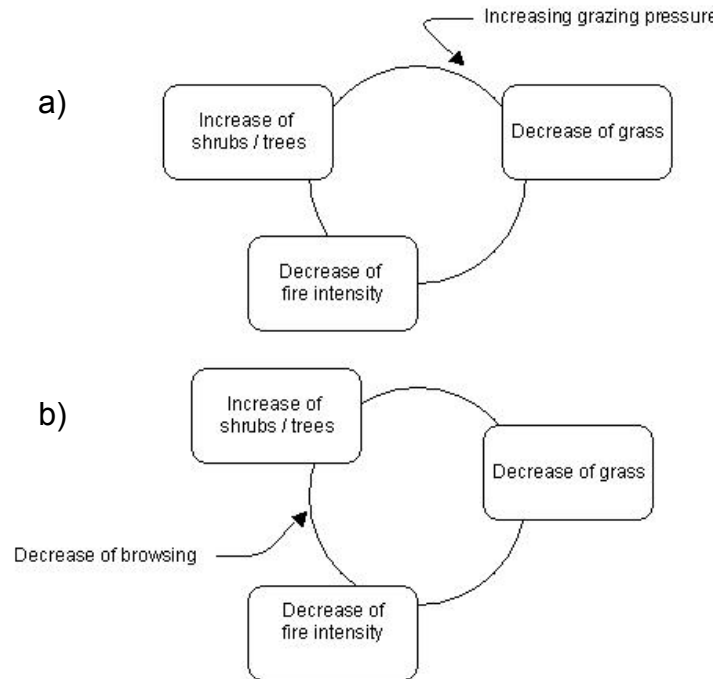
Figure 2: Positive feedback mechanism between grass biomass, fire intensity and biomass of shrubs and trees (after van Langevelde et al., 2003) when a) grazing pressure increases and b) browsing decreases.

Savannahs of Africa were present throughout the Pleistocene and steadily under semi-arid conditions. Due to this long time of presence, a broad range of species could establish even savannah have a low primary productivity (Delany and Happold, 1979).

Small mammals as model organisms

For investigating the impact of different structural assemblages on selected model organisms, the focus within this dissertation lays on small rodents in a semiarid savannah of South Africa. The use of small rodents for this study relies on two reasons. First, small rodents play an important role within savannah and desert ecosystems. As primary consumer consist their food mainly of grasses, herbs, leaves, insects and occasional fruits (e.g. Kerley, 1989; Apps, 2000). In the northern hemisphere a trend towards a higher proportion of seed intake (seed predation) happens, whereas in the southern hemisphere herbivorous and omnivorous food prevails (Kerley, 1989 and 1992). Burrowing and litter storage causes good availability of nutrition for plants

within the otherwise poor soils. Additional, small mammals are prey for a couple of predators like raptors, owl, snakes and larger mammals. Thus, they form a basic part of the trophic system.

The second reason is their good usability in studying problems related to the field of landscape – community interactions (Barrett and Peles, 1999). Advantageous are their comparable less movements and small home ranges, the good opportunities for collecting data by fieldwork (good trapability, sufficient densities and recapture rates) and their quick response to changes in the environment due to their short life cycles (Barrett and Peles, 1999).

Arboreal species are supposed responding considerably different to changes within density, quality and distribution of the structural elements and the matrix between than ground dwelling mammals do (Henderson et al. 1985; Shepherd and Swihart 1995; Lindenmayer et al. 1999; Hanski et al. 2000; Taulman and Smith, 2004). Sciurids (Wauters et al., 1994; Shepherd and Swihart, 1995; Taulman and Smith, 2004;) and muroids (Henderson et al., 1985; Hanski et al., 2000; Capizzi et al., 2003) show a population decline when the assemblage of tree species and their age distribution deviates from a natural state.

There are relative few studies on arboreal animals, probably due to their more difficult way to trap them and their comparable low densities. An additional limitation in studying arboreal animals might arise from their longevity, which often exceeds duration of funding. Nevertheless, due to its special needs arboreal small mammals seem to be suited as indicative species for assessing the quality and sustainability of certain habitats (Seamon and Adler, 1996; Taulman and Smith, 2004).

Hyotheses

Small rodents are suspected to respond sensitive to local and temporal changes within the habitat assemblages. Thus, on the example of small rodents the question is addressed: How does shrub density influence the habitat quality for small rodents? To cover a range of possible responses, this thesis aims on the occurrence of ground dwelling myomorph species as well as on an arboreal murid species (*Thallomys nigricauda*).

It has been hypothesized that:

    i)   Ground dwelling small rodents are negatively affected if perennial grass cover gets lost due to shrub encroachment.

    ii)   An increase of shrub density improves habitats for the arboreal Black Tailed Tree Rat (*Thallomys nigricauda*) due to a better connectivity among suitable structures for nesting, food and mates.

    iii)   The occurrence of bare grounds or sites covered with annual plants is considered to represent heavily disturbed areas. They do provide low-quality habitats regarding their palatability and predictability. Small rodent diversity is therefore assumed being negatively affected.

Landscape research and small mammals

Since the middle of the 1980´s, as the Landscape Ecology started to become an own ecological discipline, the studies on small mammals and their relationship to the environment increased (Barrett and Peles, 1999). A number of empirical studies on small mammals have been carried out in almost all biomes and habitats all over the world considering various environmental parameters and scales. A strong focus laid always on the consequences of habitat fragmentation and became discussed with regard to landscape use by human; often using the given situation in the field as a natural experiment (mining, clear-cuts, fire events) (Ferreira and Van Aarde, 1999; Glitzner and Glossow, 2001; Martinkova et al., 2001; Salvatori et al., 2001; Ecke et al., 2002). A further step was taken, as studies experimentally explored specific habitat characters like patch-size and shape, connectivity and horizontal / vertical diversity (Barrett and Peles, 1999, Debinski and Holt, 1999; Ims and Andreassen, 1999). Those studies provided the base for theoretical approaches (e.g. Wiegand et al., 1999; Amarasekare and Nisbet, 2001; Vandermeer and Carjaval, 2001).

Two habitat parameters have been recognized as relevant (of course, not the lonely ones) to small mammalian species diversity: the vertical diversity expressed as the number and extent of strata (complexity) and the horizontal heterogeneity within a habitat (patchiness; August, 1983). Some studies conducted at boreal habitats showed positive relationships of species diversity to complexity (Adler, 1987; Dooley and

Bowers, 1996; Horváth et al., 2001; Ecke et al., 2002). At grasslands and deserts small rodents respond positively to attributes like coverage and a certain degree of heterogeneity (Rosenzweig and Winakur, 1969; August, 1983; Kotler, 1984; Kerley, 1992; Shenbrot, 1992, Kotler et al., 1993; for a review see also Tews et al., in press). The niche requirements and potential responses of grassland small mammals are not always that obvious than in richer structured habitats. Caused by a lack of several height strata, niche separation may happen along body mass and behavioural aspects (Kerley, 1992).

A central challenge in the field of landscape ecology is the scale and resolution used to identify processes because different patterns may appear at different spatial and temporal scales (Bissonette, 1997). Animal ecologists consider the home range of a species as a useful (but not final) "grain" to look for determinants of their occurrence (Bowers and Barrett, 1999). All resources necessary for survival and, most desirable, for reproduction must be available within. Thus, the studies presented within this dissertation focus on a spatial extent matching approximately the home range size of the particular species under consideration.

A general note

One important advantage of using small mammals for investigating questions addressed to landscape ecology is the commonly good state of knowledge on their biology and ecology. Unfortunately, this was not given for the Black Tailed Tree Rat (*T. nigricauda*), since data available derive from loose observations and laboratory studies. My colleagues and me had first to provide basic data prior to evaluating habitat features. Consequently, this dissertation is of an empirical nature rather than conducting many-fold replicated experiments. For controversy discussion on this issue see both Hurlbert (1984) and Oksanen (2001).

3.2 Study area

Geography and rain

The Kalahari Basin extends from southern Africa to the South of Angola at a height of 800 to 1.200 m above sea level. Since the Cretaceous aeolian sediments became deposited and cover recently the underlying geological layers up to 500 m. Annual

precipitation reaches from 500 to 800 mm in the North, to 150 mm in the Southwest (Adams et al., 1996).

The studies were conducted at the Molopo Nature Reserve (S 25° 50′ and E 22° 55′; North West Province, Republic of South Africa, fig. 4). At the study area the surface is a gently rolling plane at 1.000 m a.s.l.. The mean annual precipitation is 332 mm (SD = 158; n = 50), falling mainly during the spring and summer months (fig. 3). The resulting CV of 38% of annual rainfall indicates a reasonably unpredictable pattern among years (30 - 45% in the winter rainfall Succulent-Karroo; 33 - 63% in the summer rainfall Nama-Karroo; Kerley, 1989). Day temperatures usually exceed 45 degrees in summer and reach 30 degrees in winter. During the night temperatures are around 20 to 25° in summer but may drop below zero degrees in winter.
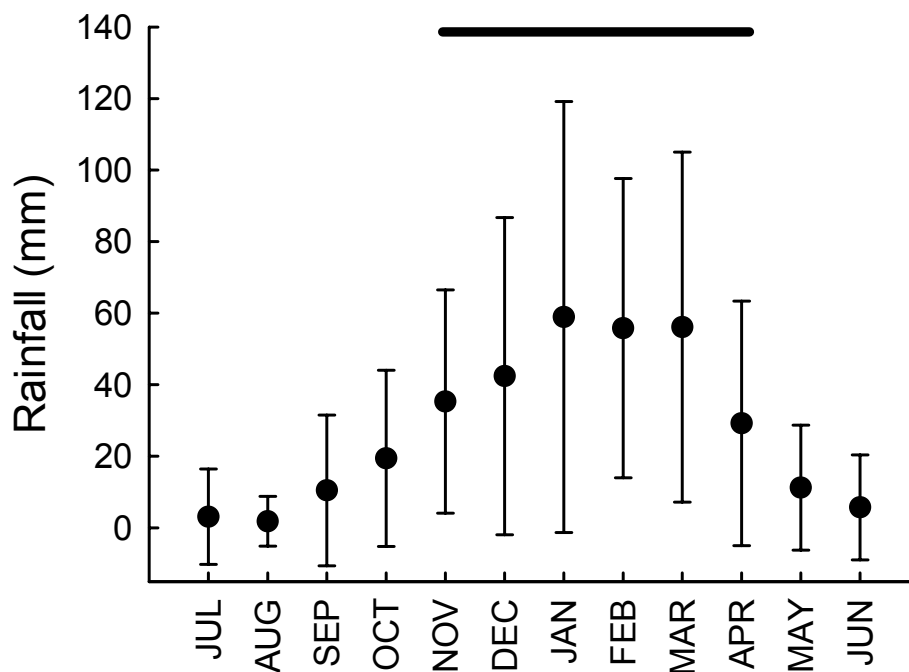
Figure 3: Mean annual rainfall at Vorstershoop (1952 – 2002; n = 50), North-West-Province, South Africa. Bars indicate standard deviation; the horizontal black bar at the top shows the time span of vegetation growth.

Vegetation

This part of the semiarid Kalahari is naturally covered by an open woodland savannah signed as the Thornveld (Acocks, 1988). The vegetation is a mosaic of trees and patches of shrubs within a matrix of perennial grasses (e.g. *Aristida, Eragrostis, Stipagrostis*). Trees can reach heights up to 10 m. Most common are the evergreen trees *Acacia*

erioloba (Camelthorn) and *Boscia albitrunca* (Shepherds Tree). Occasional the (deciduous) *Terminalia sericea* (Silver Cluster Leaf) can be found, especially at disturbed areas like former settlements. Shrub layer consists dominantly of *Acacia mellifera* (Black Thorn) and *A. luederitzii* (False Umbrella Thorn), which are the dominant encroacher plants at that area (Totlolo, 1999). Further common shrubs are *Grewia flava* (Raisin Bush), *Dichrostachys cinerea* (Sickle Bush), *Ziziphus mucronata* (Buffalo Thorn), *Rhus* sp. and *Grewia* sp.. Rarely specimens of *A. hebeclada* (Candle Thorn) and *A. haematoxylon* (Grey Camel Thorn) can be found. Thorny shrubs may develop thickets, which cannot be entered by larger animals. Additional, no grass grows under the canopy and around *A. luederitzii*. Therefore, land users do actively remove shrubs to maintain grass cover for cattle. The wood of larger trees, especially *A. erioloba* is used for charcoal burning and selling firewood. Young specimens (< 3 m) of *B. albitrunca* are frequently cut during winter or became forced to grow close to the bottom, providing shade and additional food for domestic stock.
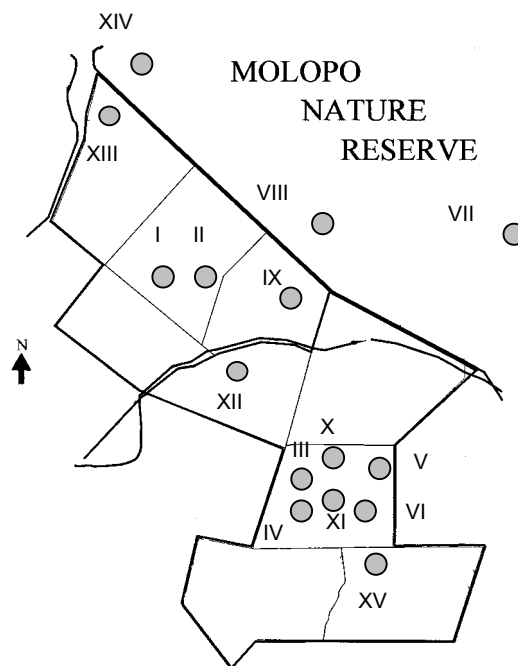

Figure 4: Map of the Molopo Nature Reserve (North-West-Province, South Africa). Increasing roman numbers sign study sites (circles) according to the relative abundance of the Black Tailed Tree Rat (high numbers = high abundances).

History of the area

Until the 1960´s, the study area was Bushmen (San) land (Godwin, 2001). As drilling techniques improved, deep groundwater became accessible and farmer begun breeding cattle and game. Thus, a comparable initial state of land use is present at the area. Stocking rates are about one cattle per 13 to 15 hectares. Farm sizes ranges from about 3.500 ha up to 10.000 ha and more.

The Molopo Nature Reserve consist of 9 former farmlands, which were operated until begin of the 1980´s for cattle breeding. The whole Reserve (240 km^2) is fenced and stocked with a variety of antelopes, including grazers and browsers. Large predators like cheetah and leopard occur at low densities. Game stock is regulated by captures for other Reserves and Parks as well as by hunting. Except occasional burnings, no human management is done on the vegetation.

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Heterogeneity and predictability of habitats and the small rodent community in the Thornveld savannah, South Africa.

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The general performance of small, ground-dwelling rodent community in a savannah ecosystem (Kalahari Thornveld, South Africa) was analysed regarding habitat heterogeneity and the predictability of four habitat types. Live trapping was conducted on sites classified either as covered by annual grasses (low predictability), sites with perennial grass (high predictability but low structural diversity) and two habitat types with a mix of grass, shrubs and trees (predictable and heterogeneous). Within 751 trap nights 85 small mammals of 7 species were caught. The most abundant species were *Tatera leucogaster* (Bushveld gerbil), *Saccostomus campestris* (Pouched Mouse) and *Aethomys namaquensis* Namaqua Rock Mouse), showing large niches breadths. With the exception of *Desmodillus auricularis* (Short Tailed Gerbil), all small rodents showed a positive response towards perennial grass cover and a negative influence of sites dominated by annual plants, which are considered a sign of disturbances. Structural diversity (H) and the presence of perennial grasses had a positive impact on the relative abundances, number of species and species diversity. The Namaqua Rock Mouse preferred sites with perennial grass and a certain degree of structural elements (shrubs and trees). Disturbed sites with annual cover had lower species richness and diversity as well as relative abundances.

4.1 Introduction

At savannah ecosystems, commercial land use may initiate processes, which strongly affect two important features of a high-quality habitat for small rodents: the presence of several structures causing spatial heterogeneity and the all year usability of that particular habitat: its predictability (Lidicker, 1995).

High stocking rates of cattle or grazing game causes an increase of thorny shrubs (shrub encroachment) and as a consequence a decreases of perennial grass cover (Delany and Happold, 1979; Schultka and Cornelius, 1997; Ryan and Joubert, 1999). Secondly, at sites with high trampling pressure open soils or annual plants replace perennial (grass) cover. The presence of annual plant cover depends on a sufficient amount of rain. Considering the strong variations of total rainfall among years, annual plant cover occurs in an unpredictable way (Kerley, 1992). Sites with annual plants might keep bare grounded during winter and in years with low rainfall. Although annual plants are present for a comparable short time and are usually of low palatability, they potentially do provide temporary habitats (Rogovin et al., 1994; van Rooyen, 2001). In contrast, shrubs provide predictable structures for years.

Small ground dwelling mammals need coverage for food and hiding. Certain degrees of coverage and landscape structures cause a considerable number of species occurring within grasslands, which in turn are directly affected by changes within the vegetation composition (Rosenzweig and Winakur, 1969; Delany and Happold, 1979). The present study analyses the small rodent community assemblage along a heterogeneity gradient from annual dominated sites over sites covered by perennial grass to areas with a mixed cover of grass, shrubs and trees at a semiarid savannah of Southern Africa.

4.2 Material and Methods

The vegetation at the Molopo Nature Reserve (S 25° 50´ and E 22° 55´; 1000 m a.s.l.) and adjacent farmland consists of an open woodland savannah belonging to the Thornveld type (Acocks, 1988). The area is a sandy, gently rolling plain, and therefore study sites were not discriminated with respect to topography and soil.

Exceptionally good rainfalls at the Kalahari North of Vryburg (South Africa) started at the middle of September 2001. The study area received a total of 588 mm during spring

and summer, while the annual is about 330 mm. Several areas, which were covered only by a few creeping plants like *Tribulus* sp. (Devil thorn) during the summers 2000 and 2001 became totally covered by either *Schmidtia kalahariensis* (Kalahari Sour Grass) or *Chenopodium album* (Goosefoot).

Trapping was carried out in mid-summer 2002 from January to March. Twenty-six trapping sites have been chosen along a 25 km transect throughout the reserve and on three recently used farmlands. Trap grids were set not closer than 100 metres distant to one another and to obvious borders of habitat types. As home ranges of small mammals are usually between 0.5 and 2 (4) ha (Christensen, 1996; Apps, 2000), a minimal distance of 100 m between the grids was considered an acceptable compromise to overcome pseudo-replication and autocorrelation regarding the circumstances at the study area (see also Hurlbert, 1984; Rosenstock, 1996). Each grid consisted of 20 (5 by 4 array) up to 36 (6 by 6 array) foldable traps (7.5 x 9 x 23 cm; H. B. Sherman Traps, Inc., Tallahassee) spaced at 10 m and baited with a mixture of oats and peanut butter. Traps were set for one night at dusk and checked at dawn. Captured animals were determined for their species, sexed and checked for their reproductive state (perforate vagina, scrotal testes). Trapping data were standardised to captures per 100 trap nights, furthermore referring to as relative abundance. Communities of certain grids were assessed using Hill´s N_2 (species diversity) and Simpson´s measure of evenness (1/D), respectively. Both indices are most sensitive to common species. The variety of habitats used was assessed by Hurlbert´s standardised niche breadth (Krebs, 1999).

Habitat structures were recorded at each grid using a hand-held satellite receiver (GPS, WGS 84 coordinates). Grass coverage (annual / perennial) was estimated for each quadrant and averaged across the particular grid. Woody plants were assigned to species. Studies, on small mammals from the temperate zones, show species diversity tending to increase with habitat complexity (MacArthur and MacArthur, 1961; August, 1983; Horváth et al., 2001), rather than floristic diversity (Rosenzweig and Winakur, 1969; Kerley, 1992). Thus, plants were classified into strata (<1 m, >1 - 5 m, and >5 m) and their relative abundances are given as density per hectare. The Shannon-Wiener index (H; on log2) was used to describe structural diversity. This index is sensitive to rare variables and gives an appropriate weight to wooden structures. As data could not be normalised by standard transformation, non-parametric correlation analyses (Spearman´s correlation on Ranks) were applied to illustrate associations among particular species, habitat variables and community measures.

Habitats were divided into four categories and each grid became subjected to one of them. According to findings from the Karoo (Kerley, 1992), mixed habitats have been grouped by the percentage of grass cover.

annual grassland:	≥ 70 % total coverage by annual grass / herbs, few shrubs / trees (4 grids in *S. kalahariensis* and 2 in *C. album*; number of grids N = 6);
perennial grassland:	≥ 70 % total coverage by perennial grass, few shrubs / trees (N = 5; 4 of them analysed, see below);
mixed, open sites:	< 30 % grass, shrubs and trees present at different densities (N = 7);
mixed, covered sites:	≥ 30 % grass, shrubs and trees present at different densities (N = 8).

4.3 Results

Within a total of 751 trap nights 85 small mammals of 7 species were caught. The most frequently trapped species were the Bushveld Gerbil (*Tatera leucogaster*, n = 28), the Pouched Mouse (*Saccostomus campestris*, n = 25) and the Namaqua Rock Mouse (*Aethomys namaquensis*, n = 22). The Hairy Footed Gerbil (*Gerbillurus paeba*) and the Short Tailed Gerbil (*Desmodillus auricularis*) were captured 4 times each. Only one Highveld Gerbil (*Tatera brantsii*) and an Elephant Shrew (*Elephantulus intufi*; macroscelids) were caught and omitted from further analyses. One sampling site within perennial grassland was also rejected from analyses because Black Backed Jackals (*Canis mesomelas*) had learned to open the traps.

Highest relative abundances of small rodents were recorded at grids with sufficient coverage of perennial grasses and such with mixed vegetation. Even not significant, relative abundances were lowest at sites covered with annual plants (tab. 1). Niche breadths are large within the three most abundant species, showing a considerable overlap among all species analysed (fig. 1). The number of species within the community was estimated on 4.1 species (r^2 = 0.99; SE = 0.006) by applying the rarefaction estimator on a theoretical sample size of 20 individuals.

Table 1: Relative abundances (individuals per 100 trap nights ± SD) of five small rodents species within four habitat categories. The numbers of trap nights are given below habitat names in parentheses.

	Annual (140)	Perennial (142)	Mixed open (190)	Mixed covered (279)
T. leucogaster	2.1 (± 2.4)	5.6 (± 8.3)	4.2 (± 2.0)	3.2 (± 2.9)
S. campestris	4.3 (± 2.6)	4.2 (± 1.6)	4.2 (± 5.7)	1.8 (± 2.6)
A. namaquensis	0	1.4 (± 2.9)	1.6 (± 3.3)	6.1 (± 3.8)
G. paeba	0	2.1 ± 2.7)	0	0.4 (± 1.0)
D. auricularis	1.4 (± 4.1)	0.7 (± 1.4)	0.5 (± 1.1)	0
Total (± SD)	8 ± 4.6	14.2 ± 8.6	11.3 ± 5.7	11.8 ± 6.4

The most abundant species *T. leucogaster* and *S. campestris* showed no significant associations with habitat variables, while the Namaqua Rock Mouse (*A. namaquensis*) is obviously connected to a certain degree of shrubby cover and thus, heterogeneity within the vegetation structure (Tab. 2). All individuals of *G. paeba* were caught at sites covered by perennial grasses between 24 and 90 %, which gradually differs to findings from the Karoo / South Africa (Kerley, 1992). Correlations of community measures to habitat features indicate a preference for the presence of perennial structures. A positive impact of structural diversity (H) on the community measures can be shown. Note, that significant results disappear if the Bonferroni correction is applied table wide.

Table 2: Results of pairwise correlations (Spearman´s R) of relative abundances of small rodents and community measures versus wooden vegetation height, grass cover and structural diversity at the Thornveld savannah. (+ or - indicate r-values between zero and the (positive / negative) critical r for the one tailed tests [about r = 0.3]; ++ or – above ± 0.3). Asterisk show significance at p = 0.05.

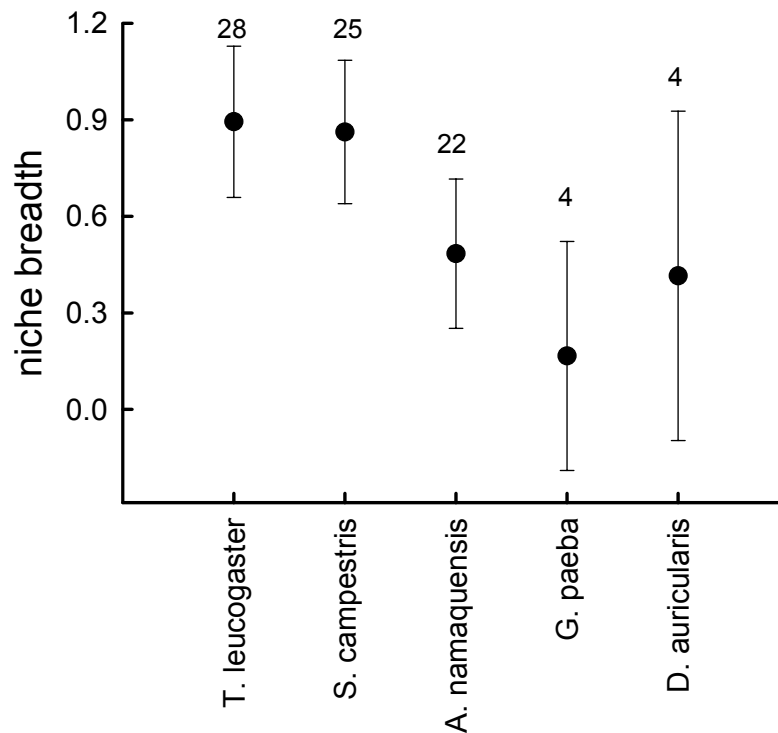|	Stratum < 1 m	Stratum > 1-5 m	Stratum > 5 m	Annual grass	Perennial grass	H
T. leucogaster	-	-	-	--	+	-
S. campestris	+	-	++	-	+	+
A. namaquensis	+	++ *	-	-- *	+	++
G. paeba	-	-	-	-	++ *	-
D. auricularis	-	-	++ *	+	-	-
Number of species	+	+	+	-- *	++ *	+
Relat. Abundances	+	+	+	-- *	++ *	+
Hill´s N_2	+	+	+	--	+	+
Evenness	-	-	+	+	-	-

Figure 2: Hurlbert´s standardized niche breadth in 5 small rodents from the Thornveld savannah basing on four habitat categories. Errors bars show standard deviation, numbers above give the amount of individuals captured.

4.4 Discussion

According to distribution maps, a total of 13 (Apps, 2000) respective 14 (Stuart and Stuart, 2001) species of small rodents potentially occur at the study area. An internal checklist of the Molopo Nature Reserve claims *Mus indutus* (Desert Pygmy Mouse) and *Steatomys pratensis* (Fat Mouse) occurring there, which is contrary to available distribution maps (Apps, 2000; Stuart and Stuart, 2001). Also the presence of *Aethomys chrysophilus* (Red Veld Rat) is considered differentially (Chimimba et al., 1999). Consequently, this study covers between 43 to 55 % of the potential small rodent community. Considering the variety of habitats, the extent of the sampling sites and the duration of the study, I argue to have not missed any relevant part of the small rodent community. The lonely species described as diurnally active is the Striped Mouse (*Rhabdomys pumilio*), which might probably not been caught due to our crepuscular and nocturnal trapping regime (Gliwicz, 1985).

As Kerley (1992) argued, the considerable high number of species in a low to medium productive biome as the semi-deserts and savannahs can be achieved by separating species by size and behaviour (but see Bowers and Brown, 1982). The five rodent species within the study presented are considerably differentiated in size and / or preferred food (Apps, 2000; Stuart and Stuart, 2001). An overlap in the body weight and food taken in *D. auricularis* and *A. namaquensis* is compensated by different habitats used.

Three of the five species studied show a large niche breadth. Caused by that wide range of suitable habitat features, no strong associations among the community measures and the habitat variables exist. Nevertheless, our general finding of preference for sites with perennial grass and therefore with a predictable cover for longer time spans is consistent with similar studies in grassland ecosystems (Shenbrot, 1992; Rosenstock, 1996; Withford, 1997; Joubert and Ryan, 1999). In savannah and grassland ecosystems, predictable (grass) cover seems to be a crucial factor for attractive habitats (Adler, 1995; Nyako-Lartey and Baxter, 1995; Fuller and Perrin, 2001). Small rodent mammals of the deserts and grasslands of the Southern hemisphere are considered to be predominantly herbivorous (Kerley, 1992). Perennial grass coverage may thus provide food and decrease predation risk (Kotler, 1984; Kotler et al., 1994). The occurrence of shrubs and trees in grassy habitats is discussed contrary. On one hand, the spatial heterogeneity increases and facilities for additional species might be expected. On the other hand, spatial heterogeneity also increases chances for competitive species and predators (´resource facilitation´ Kotler et al. 1993). Some snakes like the very common Puffadder (*Bitis aurietans*) do hunt under bushes rather than in the grass (Branch, 1998).

Because the progressing increase of shrub cover reduces perennial grasses, the process of shrub encroachment must be considered negatively for the species diversity of small ground dwelling rodents. Disturbed sites covered by annual plants appear to act as temporary, habitats and can be supposed to connect areas with perennial vegetation in years of higher precipitation. The Namaqua Rock Mouse *A. namaquensis* and the Hairy Footed Gerbil *G. paeba* seem to avoid such annual sites.

Our study gave only marginal evidence for an increase in species diversity when structural heterogeneity (H) increased. The critical element might be the optimal ratio of shrub density and perennial grass cover, providing cover and spatial heterogeneity simultaneously. The only species responding obviously positive to both, an increase of woody structures and perennial grasses, is the Namaqua Rock Mouse (*A. namaquensis*).

It is the lonely species caught several times up to 2 m above ground in shrubs and trees. A frequent use of the vertical spatial scale by other terrestrial rodents was not recorded; even this might be often underestimated in studies on ground dwelling rodents (Nordvig, et al., 2001).

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Nesting sites and nest density of *Aethomys namaquensis* (Rodentia, Muridae) in the Thornveld savannah of South Africa

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Nest sites of *Aethomys namaquensis* (Namaqua Rock Mouse) were recorded and data on their location and associated structures obtained. All nests (n = 92) were found connected to wood, acting as initialising structures for nest construction. Nest directly build on the ground had larger grassy cupolas above than such within trunks and trees. The latter were only found in the rainy summer 2002. Habitat requirements of *A. namaquensis* are described by the presence of perennial grasses and small to medium sized shrubs. At disturbed sites, frequently covered by annual plants, no nests of *A. namaquensis* have been found. Vegetation changes caused by human use may decrease (disturbed sites) or increase (increased shrub cover, dead woody remainders of cut-offs) the abundances of this small rodent.

5.1 Introduction

The Namaqua Rock Mouse (*Aethomys namaquensis* Smith, 1834) is an herbivorous small rodent, living in colonies (Gliwicz, 1987; Denys, 1994). The distributional range of *A. namaquensis* extends from the moist to the rather dry parts of southern Africa (Chimimba et al., 1999). Considering its widespread occurrence, *A. namaquensis* seems able to cope with a broad variety of habitats. Nests are reported from rocky crevices (Apps, 2000), sand dunes (Rautenbach and Nel, 1975) and tree holes (Lovegrove and Heldmaier, 1994). In this note we provide information about nest location, nest size and nest densities in correlation to vegetation structure from the Thornveld of South Africa.

5. 2 Material and Methods

The study was conducted at the Molopo Nature Reserve (S 25° 50´; E 22° 55´) during winter 2001 (August – September) and summer 2002 (January – April). The area is covered by a woodland savannah (Thornveld savannah; Acocks, 1988) with *Acacia erioloba* (Camelthorn), *Boscia albitrunca* (Shepherds Tree), *Acacia* shrubs (*A. mellifera* and *A. luederitzii*) and several species of annual as well as perennial grasses. Before the reserve was established in 1987, the area was used as farmland. At previous heavily used sites like water holes and settlements, the ground is either bare or covered by annual grasses due to grazing and trampling. The presence of a dense annual grass cover depends on rainfall (Delany and Happold, 1979).

Nests of *A. namaquensis* were recorded wherever found. Entrances of nests are covered by large amounts of dry grass. We noted height and diameter of nests as well as species, height class (<1 m; 1 to 3 m; >3 to 5 m and >5 m) and diameter of the patch or trunk, where the particular nest was situated. Nests in standing trunks were distinguished from nests on the ground. Those at the base of standing dead trees were considered as ground nests.

The correlation of nest density and vegetation was analysed across 14 sites (mean area of sites = 8.6 ha; range 1.4 – 24.2 ha) along a 30 km transect within the reserve. Vegetation structure was sampled within circles of 60 m in diameter (= two seconds; GPS, WGS 84; mean number of circles within sites = 3.8, range 2 - 9). We recorded

percent coverage of annual and perennial grass species, number of woody plant species within four height classes (see above) and number of ground-lying dead wood (fallen trees or cut shrubs; see below). Estimates were averaged for each site. Prior to all analyses, data were transformed (counts: square root; percentages: arcsine; Zar, 1999). Principal component analysis (PCA; based on the correlation matrix) was used to summarize variation of vegetation structure across sites. Judged by the shape of the screeplot we extracted three principal components (ter Braak, 1995). PC scores of sites with and without nest were tested for differences using t-tests.

5.3 Results and Discussion

All 92 nests found were associated with trees or trunks. Most nests (n = 56) were situated on the ground, while we found 36 nest in standing trunks or trees. The latter were exclusively found in 2002, a year with rainfall above the average (588 mm, mean = 320 mm). Nests on the ground were built within cut *Boscia albitrunca* and trunks of large, fallen trees (Tab. 1). Small individuals of *B. albitrunca* are frequently cut by farmers and left in the field to provide food for domestic stock during winter.

Table 1: Percentage of structures used for nesting by *A. namaquensis* in the Thornveld savannah (South Africa). All shrubs / trees on the ground were dead.

Species / height class	Ground (n = 56)	Trunk (n = 36)
B. albitrunca >3 to 5m	23	17
A. erioloba >3 to 5m	4	6
A. erioloba > 5m	0	14
Dead trees >3 to 5m	9	8
Dead trees > 5m	30	19
Unknown	34	36

It is difficult to estimate the total size of nests, as they may spread considerably below the grass cover of the entrance. Nevertheless the mean volume of the grass cover may give a hint on total nest size. The mean volume of ground nests (2/3 π x radius x nest

height) was 503 litres (SD = 284; n = 38). The volume of the grassy cupola was neither correlated to the diameter of the trunk (mean = 34 cm, SD = 8.8; n = 26) nor to the patch diameter of cut shrubs (mean = 5.3 m; SD = 1.4; n = 24; both $r^2 < 0.01$; both p > 0.8), where the nests were located. The size of the nests within trunks cannot be estimated directly. Nevertheless the volume of the trunk section harbouring the nest gives an upper limit (mean = 122 litres; SD = 83.9, n = 22). Nests within standing trunks are thus smaller than ground nests. Nest density may reach values between 1.5 to 2 nests ha^{-1}, although on a small scale densities can be much higher. Density is positively correlated to the amount of dead shrubs and trees (mostly cut by farmers) and negatively correlated to the amount of annual grass cover (Tab. 2).

Table 2: Correlation coefficients of nest density versus characteristics of the vegetation and their loadings on the first three principal components (14 sites within the Molopo Reserve, South Africa). Significant correlations (p < 0.05) and loadings > 0.7 in bold. Wood on the ground mainly consists of cut B. albitrunca.

Variables	r	PC 1	PC 2	PC 3
Stratum < 1 m	0.21	**0.86**	-0.17	-0.29
Stratum 1–3 m	0.23	**0.92**	-0.34	0.02
Stratum > 3-5	0.05	-0.01	-0.45	**0.88**
Stratum > 5 m	-0.50	0.19	**0.76**	0.25
Shrub and tree cover	0.04	**0.92**	-0.16	0.3
Annual grass	**-0.63**	0.35	**0.86**	0.05
Perennial grass	0.52	-0.63	-0.68	-0.07
Wood on the ground	**0.57**	0.57	-0.48	-0.25
Eigenvalues		3.32	2.4	1.08
Variance explained		41	30	13

PC 1 summarizes the variation in the density of shrubs and perennial grass cover, while PC 2 shows variation caused by annual grass and large trees. Sites without nests (n = 4) were not different from sites with nests (n = 10; p > 0.1 for all three PC axes). Nest density was significantly correlated only to the scores of PC 2 (fig. 1; Tab. 2). PC 2 is interpreted as a disturbance gradient, as the annual grass cover increases on disturbed sites. Large trees are also rather abundant on these sites. The common variation of annual grass cover and large trees is interpreted as a result of the history of the reserve. Large trees remained untouched by the previous farmers as they provide shade for the

livestock. Hence the use of the landscape as farmland seems to have two contrasting effects: cutting trees provides structures for nest construction whereas disturbances decrease nest density.
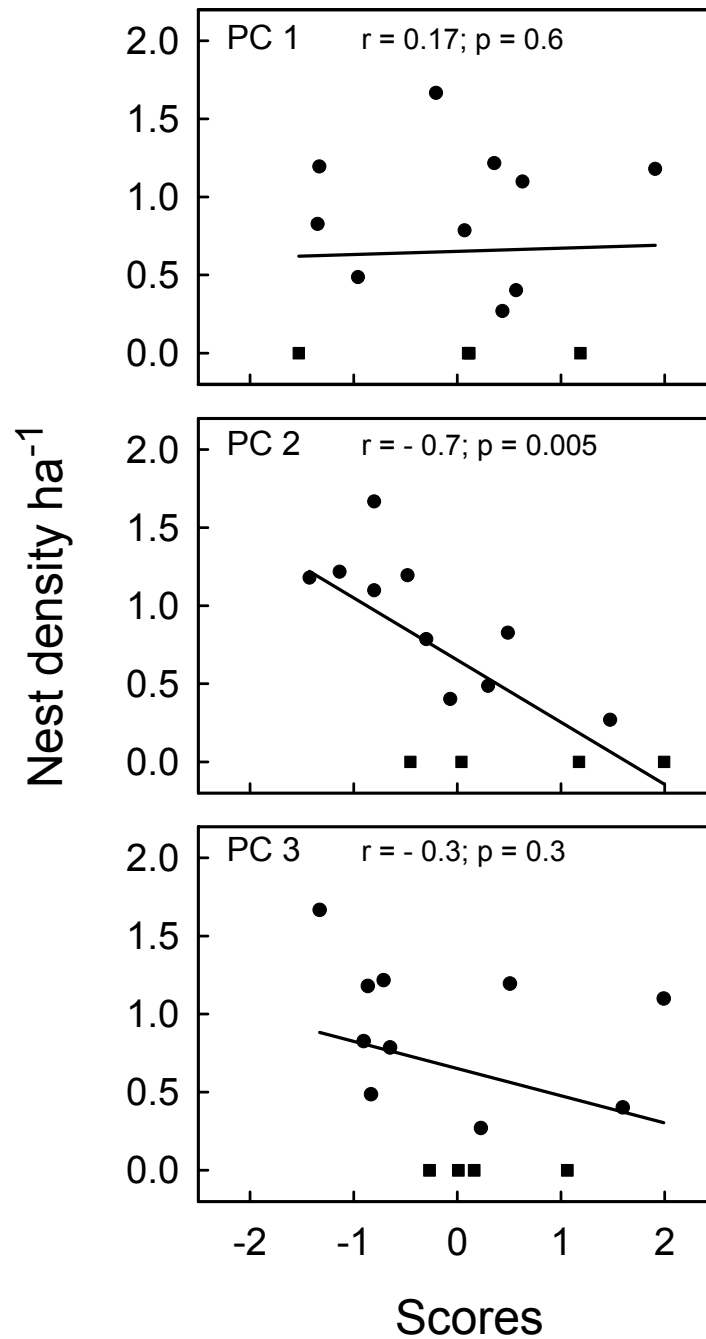

Figure 1: Plot of principal components scores (see Tab. 2) versus nest density ha^{-1} of *A. namaquensis.* Circles represent study sites with, squares without nests. Note, that density of *A. namaquensis* decreases with an increasing cover of annual grasses.

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Space use, circadian activity pattern, and mating system of the nocturnal Black Tailed Tree Rat *Thallomys nigricauda.*

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We present results of a radio-tracking study of the Black Tailed Tree Rblack at *Thallomys nigricauda*, based on 3 males and 4 females in the breeding season and 2 males and 5 females in the non-breeding season. The study was conducted in the southern Kalahari Thornveld, South Africa, a savanna landscape of *Acacia* trees and patchy *Acacia* bush. Nocturnal activity patterns, vegetation use, space use, and interactions were followed for 8 - 17 days. During the breeding season, males were active with 2 synchronous activity peaks shortly after sunset and at late night. Home ranges included the nests of 8 - 10 females, 6 different daytime resting places, and 3 - 5 areas of high activity. Males were mobile within home ranges of 5 - 10 ha (90% minimal convex polygons) that overlapped with other males, and covered home ranges of several females. Activity of females peaked shortly after sunset and before sunrise with 6 h of low activity between. Home ranges of nursing females were 0.001 - 0.03 ha, and included 2 small areas of high activity (nest and foraging site), where no other adult females were observed. Animals preferred small acacia shrubs (*Acacia mellifera* and *A. luederitzii*) for foraging. Activity of both sexes during the non-breeding season was low, with only one distinct peak shortly after sunset. Although small acacia shrubs offered only dry leaves, they were preferred by both sexes for foraging. Rats were observed feeding on buds. Home range size of males was 1 - 2 ha and of females was 0.1 - 0.3 ha. Contrary to earlier reports, we found tree rats living solitarily or with young offspring. We suggest that the species has a polygynous mating system.

6.1 Introduction

Tree rats of the *Thallomys* group are distributed widely over African woodlands and savannas (Nowak 1991) but are poorly known due to their nocturnality, arboreality and low economic impact. In southern Africa, they feed mainly on acacia trees and shrubs (Shortridge, 1934; de Graaff, 1978; Skinner and Smithers, 1990). For the two sibling species occurring in South Africa *T. nigricauda* and *T. paedulcus* (for taxonomic issues see Gordon, 1987 and Taylor et al., 1994) living in groups or colonies (Nel, 1975; Rautenbach, 1982) or one breeding pair per nest plus offspring (Smithers, 1971; de Graaff, 1981) have been reported. Previous studies on *T. nigricauda* have addressed circadian aspects of thermoregulation (Lovegrove et al., 1991; Lovegrove and Heldmaier, 1994), climbing behavior (Earl and Nel, 1976) and natural history (Meester and Hallet, 1970). But, generally little information exists for any of *Thallomys* species in the wild.

As a general rule, spatial behavior and home range size depends on body mass, energy requirements, habitat productivity and mode of locomotion (Swihart et al., 1988). Also the sex, present reproductive state and mating system affects the size of a home range used (Ostfeld, 1985; Clutton-Brock, 1989). Recently, few species of arboreal small mammals have been investigated (Hanski et al., 2000). In this study on the black tailed tree rat (*T. nigricauda*) we used live capture and radio tracking to investigate how individual tree rats use time, vegetation, and space. The analysis involved comparisons regarding sex, season, body mass, and interactions between individuals. The study was conducted in the southern Kalahari Desert of South Africa.

6.2 Material and Methods

Tree rats were studied in the Molopo Nature Reserve in the southern Kalahari Thornveld savannah, North-West Province, South Africa (25° 50' S; 22° 20'E). The reserve lies in a zone of variable annual rainfall (mean = 330 mm; SD = 159; n = 50) between September and March. The Kalahari Thornveld is a savannah landscape, composed of *Acacia* trees *A. erioloba* (Camelthorn), *Boscia albitrunca* (Shepherd´s Tree)*, and stands of *Terminalia sericea* (Silver Cluster Leaf). Common bush species are *Grewia flava* (Raisin Bush), and *Acacia* species like *A. mellifera* (Black thorn), and

young *A. erioloba* and *A. luederitzii* (False Umbrella Thorn). Trees and shrubs form distinct patches with sandy soil between. Grass cover varies between years and seasons. Nests and resting places of tree rats were identified by searching stems and bases of trees for feces and the distinctive smell of excrements. Single-capture traps (Sherman Inc., Tallahassee, USA) were tied to horizontal branches and baited with oats, peanut butter, and fruit jam (de Graaff, 1978). On capture, rats were sexed and weighed. Rats heavier than 45 g were fitted with a radio transmitter (Biotrack, Wareham, United Kingdom). Transmitters weighed 1.4 - 2.0 g (2 - 4% of body mass) and had at least 21 days of battery life. Tracking was conducted on foot with a hand-held antenna. Grid coordinates of the location of an animal at one point in time (fixes) were recorded by using a handheld GPS (Garmin Int. Inc., Kansas, USA). Plant species or structures (trunks of dead trees) were determined when we were 3 - 10 m from the animal. Fixes at already known locations were confirmed with angular bearing from $20 - 30$ m without close approach to the animal. Tracking was conducted mainly at two sites approximately 1 km apart. Site A was a shrubby area with a lower density of suitable nesting trees, mainly *B. albitrunca* and a few *Acacia*. Density of tree rats at site A was probably higher than at site B since we captured more rats there with less trapping effort. Site B had many nest in large *Terminalia* and *Acacia* trees.

During the breeding season, animals were studied for 3 weeks in February - March 2001. Temperatures were about 25 degrees at night and $30 - 45$ degrees during daytime. Dusk and dawn lasted 40 min each. Plants had green foliage. At that time *A. erioloba*, *A. luederitzii* and *G. flawa* were flowering or fruiting. At site B we captured two adult males, heavy enough to be radiotagged and one sub-adult female (40g, vulva closed; Champlin et al., 1973). We captured two more adult females at site B. At site A we captured and tagged one adult male with scrotal testes, one nursing female, and a smaller, non-nursing female (Tab. 1). Two more adult females and one young male were captured during the radio-tracking study. At two additional sites we additional captured and tagged two nursing females. Sites were separate and 0.5 km and 1 km away from both sites A and B, respectively. Rats were followed for 9 - 17 days, although not successively, because home ranges of males exceeded the range of transmitters. One individual had to be recaptured and fitted with a modified collar with a lengthened antenna. At the end of the study, all animals were recaptured and tags were removed.

During the non-breeding season, tree rats were studied for two weeks in August - September 2001, at the end of the dry season. Temperatures were –1 to +5 °C at night and 10 - 30 C during the day. Only *A. erioloba* and *B. albitrunca* had green foliage. Acacia shrubs of *A. mellifera* and *A. luederitzii* offered dry leaves, but occasionally started flowering towards the end of the study period. We tagged all animals captured at site A. Some females had open vaginas, but no female was lactating. Two adult scrotal males, four adult and one small female, were monitored over 8 consecutive days.

Table 1: Home range size of Black Tailed Tree Rats (*T. nigricauda*) measured by radio telemetry during an 8-d tracking period. MCP, minimum convex polygon; Ranges of values are given. In the non-breeding season, one female was always tracked at the same location so her home range size was 0 (given in parentheses).

Season and sex	N	Reproductive condition	Weight (g)	MCP (ha)		85% activity cores		No. day hides
				100%	90%	Size (ha)	No.	
Breeding								
Males	3	Scrotal	70-90	5.9 – 11.5	4.9 – 10.2	0.3 – 1.7	3-5	6
Female	1	Subadult	50	1.1	1.0	0.012	3	2
Females	3	Nursing	90-95	0.02 – 0.17	0.001 – 0.03	0.002 – 0.005	2	1
Non-breeding								
Males	2	Scrotal	70-75	1.9 -. 3.2	1.5 – 1.7	0.1 – 0.4	2-3	2-3
Female	1	Subadult	45	0.12	0.12	0.003	3	1
Females	4	Adult	53-70	(0), 0.1 – 0.5	(0), 0.1 – 0.3	(0), 0.002 – 0.03	(1) 2	1

Rats were always inactive during the day. For circadian activity profiles, nights from 1800 h to 0700 h were divided into 13 hourly intervals. We visited each rat on 2 - 3 different nights in every interval (average 2.4 visits per animal per interval). Activity of the animals was determined by listening to the strength and amplitude of the ratio signal

from a distance of 30 - 50 m without disturbing the animal. Rats were considered to be active if at least on of the following case were recognized: i) signal amplitude from the transmitter was fluctuating (indicating that animal was moving, which affected the position of the transmitter relative to the observer); ii) animals were observed moving or feeding; iii) the signal or observation was from a tree shrub too small to have a nest in its trunk; or iv) if its location had changed during the since the last bearing. Rats were considered to be inactive if signal amplitude was constant and came from within a tree trunk.

Use of vegetation was analyzed by comparing the availability of plant species with fixes on that plant species, using only active fixes. Fixes were pooled for sex and season. To quantify vegetation, we counted individual shrubs and trees within circles of 60 m in diameter (= two seconds of WGS 84 coordinates). At site A we chose two random circles. At site B we chose locations within home ranges: two frequently and two rarely visited. Values were averaged across circles for each site.

Home range sizes and overlaps were calculated using RANGES V software (Kenward and Hodder, 1997). To minimize autocorrelation, we used fixes taken at least 2 h apart. We used up to 4 fixes per night plus the daytime location. To be able to compare the data between seasons, we used the largest number of tracking days per animal available from both seasons, thus omitting some of the data from the breeding season. Resulting data consisted of 8 days and nights with an average of 30 (SD = ± 4.0) fixes per animal. We calculated minimum convex polygons (MCP, Kenward, 1997) including 100% of fixes to determine the maximal area used. Ninety percent MCP were calculated to exclude occasional excursions. In both seasons females always used the same daytime resting place, thus fixes furthest from the nesting tree were excluded for the 90% MCP calculation. For males without a single nesting tree, fixes furthest from the harmonic mean (based on the density distribution of all fixes) were excluded. The polygon method is sensitive to sample size. To determine adequate sample sizes, range size was plotted against number of fixes (Harris et al., 1990). In our data (fig. 1), 90% of the total area was attained for different males with 12 - 27 (mean = 19) fixes. Home range size was stable at 16 - 27 (mean = 25) fixes, reaching an asymptote with ~30 fixes. For females, 90% of area was attained with 5 - 31 (mean, 28) fixes, but an asymptote was not reached. In such a situation, it may be preferable to present a home range estimate based on a standard number of fixes, close to the value at which most home range estimates reach an asymptote (Harris et al., 1990), as we did by using all ~30 fixes.
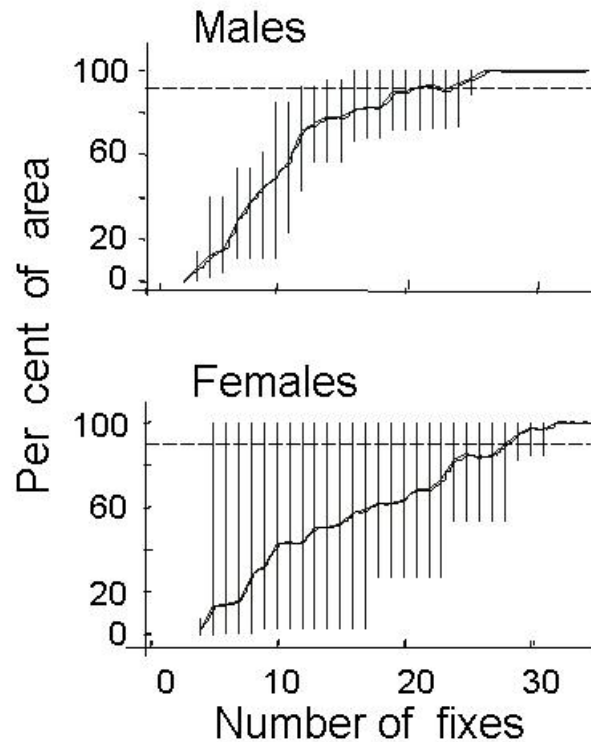
Figure 1: Cumulative area plot for *T. nigricauda* using 100% minimum convex polygons. Curves represent mean areas reached by several animals, and vertical bars the range of values at each fix (locating an individual). Dashed line shows 90% of the area. On average, 90% were reached with 27 fixes for females (n = 9 females) and 19 fixes for males (n = 5 males). All females reached 100% of the area at 31 fixes and all males at 27 fixes.

To define core areas of high activity, cluster analysis based on nearest-neighbor distances between fixes were conducted (Kenward, 1987). We included only fixes where Black Tailed Tree Rats had been active (Harris et al., 1990) in the analysis (17 ± 5 fixes per animal). Cores were based on 85% of active fixes, excluding outliers that would substantially increase the proportional use of area as determined by a utilization distribution of cluster analysis. An increase in the proportion of the maximal area used was compared between differently sized clusters. We compared clusters containing 60% to 95% of fixes in 5% steps (Kruskal-Wallis H-test for 8 clusters of 13 animals: H = 61, p < 0.001 [1 female, with only 1 fix location was excluded from this analysis]). There was no increase in the proportion of area between 60% and 85% clusters of fixes (post hoc Tukey's, p > 0.820), but there was a significant increase between clusters of 90% and 95% (post-hoc Tukey's, p < 0.001).

One-way analysis of variance was used to compare the 4 groups defined by sex and season. Groups were compared post-hoc by Tukey's test, with harmonic mean samples creating homogenous subsets. If variances were not homogenous, non-parametric analyses were carried out. Statistic analyses were conducted with SPSS 10.1 (SPSS Inc., Chicago). Values are presented as mean ± SD.

6.3 Results

Activity pattern

The proportion of active fixes was slightly (though insignificantly) higher for male tree rats in the breeding season (0.69 ± 0.24) compared to all other combinations of sex and season (0.44 ± 0.09 for males in the non-breeding season; 0.43 ± 0.06 for females in the breeding season and 0.42 ± 0.06 for females in the non-breeding season; $F_{3,10} = 3.0$; $p = 0.08$).

All groups displayed activity patterns with a distinct peak in the early night (Fig. 2). In the breeding season the peak lasted longer (1900 - 2200) than in the non-breeding season (1800 - 2000) and showed a second peak near the end of the night. Male activity decreased slightly from 100% activity in the early evening to > 50% around midnight and peaked again to ~90% at 0300 h. Nursing females resumed activity earlier than males (20% were active before dusk, compared with no activity by males at that time). Their bimodal activity pattern was more pronounced, showing an early night activity peak of 80% and also an 80% activity level at dawn (11% for males). Between peaks, activity was lower (20 - 40 % from 2200 - 0400 h), than male activity was (50 - 60% from 2200 –0300 h). In the non-breeding season, activity of males had a short peak (100% for one hour after dark) and zero activity at midnight. Female activity was more evenly distributed over the night with 25-60 % of animals active each hour (fig. 2).

Vegetation use

Males used several different resting places (trees) within their home ranges during the day (Tab. 1), whereas adult females used only one nest in both seasons. Fifty-four percent of the trees used for during the day were dead *A. erioloba*; with 32% dead *Terminalia* and 14% live *Boscia* trees ($n = 29$).
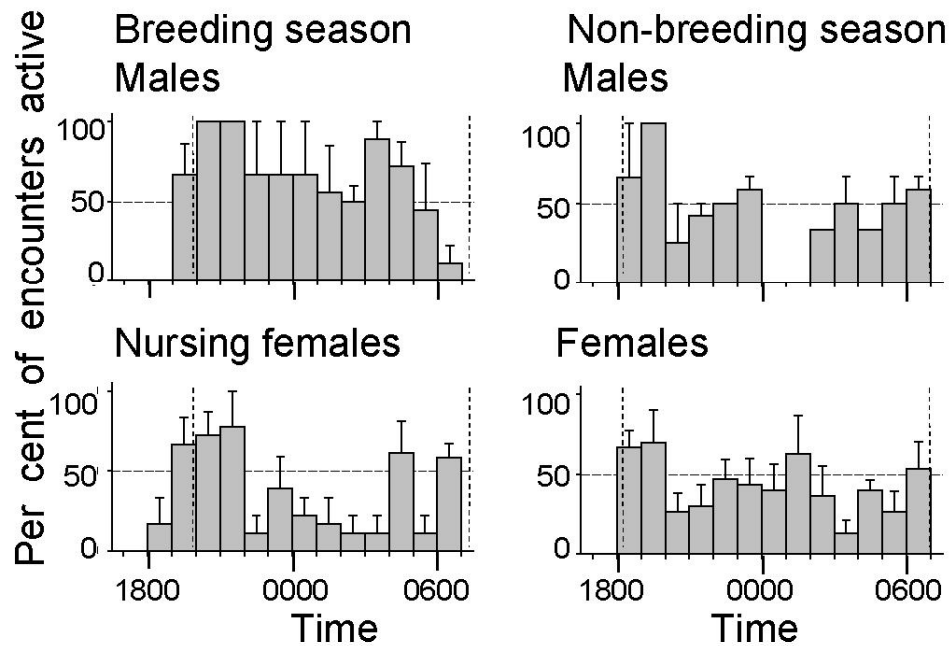
Figure 2: Nocturnal activity profiles of Black Tailed Tree Rats (*T. nigricauda*) in breeding season (3 males; 3 females) and non-breeding season (2 males; 5 females). Bars show means and SE of the percentages of fixes that animals were active in a 1-h interval. Dashed lines indicate sunset and sunrise.

Foraging tree rats favored *A. mellifera* and *A. luederitzii* shrubs. Nursing females foraged relatively more often in those species (16 of 18 fixes were in *Acacia,* while the count of available individual plants revealed a smaller proportion of *Acacia* shrubs (100 out of 230 total shrubs and trees); $\chi^2 = 11.8$; d.f. $= 1$; $p < 0.001$). During the non-breeding season, *Acacia* shrubs were preferred for foraging by both sexes (37 respective 41 fixes at Site A, $\chi^2 = 28.1$; d.f. $= 1$; $p < 0.001$). There were no differences between preferences of males (10 out of 11 fixes) and females (27 out of 30, Fishers exact test, $p = 1.0$) in the non-breeding season. Animals were easily observed foraging on buds in shrubs without foliage. Gnaw marks were found in the bark of lower branches of some frequently used individual *A. mellifera*. Non-foraging activity of males in the breeding season was not preferentially in *Acacia* shrubs (22 to 43 fixes, sites A and B combined, $\chi^2 = 0.2$; d.f. $= 1$; $p = 0.6$).

Home ranges

Home-range size (Tab. 1) differed among combinations of sex and season for 100% and 90% MCP and 85% activity cores (Kruskal-Wallis test; d.f. $= 3$; H $= 9.6$; $p = 0.02$; and

H = 9.6; p = 0.02; and H = 8.9; p = 0.03). Home ranges (MCP) of males in the breeding season were significantly larger than for all other groups (post-hoc tests for homogenous subsets, p < 0.001). Males also had larger core areas of high activity than females (both seasons pooled; n = 5 and 9; Mann-Whitney U = 0; p < 0.01). Adult females always used two activity cores: one at the nest and one at a preferred feeding site. Males and sub-adult animals used different daytime resting places in addition to 2 - 5 sites of high activity (Tab. 1). During the non-breeding season, one female was repeatedly located at only one site; therefore her home range was estimated at zero and number of activity cores as one (female F1; fig. 3).
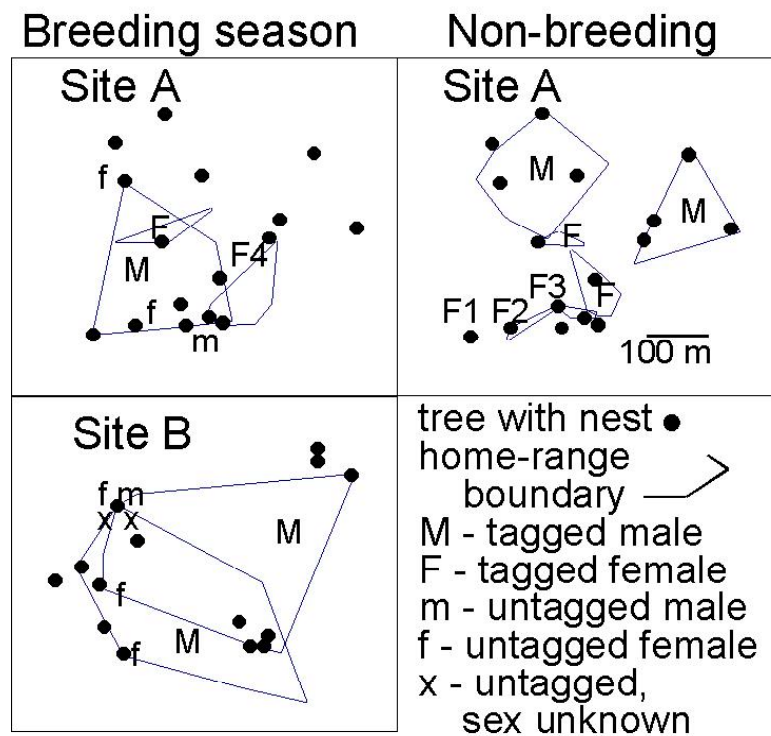

Figure 3: Home-range estimates for *T. nigricauda* in breeding and non-breeding season. Site A had a higher density of suitable nesting trees than site B. Untagged females (f) were resident throughout the study period; untagged males (m) were probably transient. The tagged female F1 was repeatedly located at one site only; F2 (subadult) and F3 (adult) were captured in the same nest, F4 was a subadult animal.

Interactions between tree rats

Within the breeding season, the home ranges of male at site A overlapped with home ranges of both tagged females (overlap 44% and 9%, respectively, of 100% MCP; fig. 3). Activity cores did not overlap. One young male was repeatedly captured within the tagged male's home range. We also captured one other nursing female and identified nine potential nesting sites within the males' home range. Home ranges of two tagged females did not overlap (fig. 3). Home ranges of 3 nursing females (site A plus the two separate sites) never included another nest than their own, and we did not observe or capture any other females within the home ranges.

At site B, home ranges of both males averaged 47% in mutual overlap (100% MCP; fig. 3) and 21% in mutual overlap of activity cores. Three females were observed or captured within home ranges of the males. We identified up to 10 potential nesting sites of females within the males' home ranges (fig. 3). Once in the early night we observed an untagged female mating with a tagged male. Nearby, another untagged male, a second tagged male, and 3 other untagged adult tree rats of unknown sex were present (fig. 3). During the non-breeding season at site A (fig. 3) 100% MCP of a male and a female overlapped slightly by 2%, but their activity cores did not. The small female (F2 in fig. 3) and a female of average size (F3) were captured in the same nest. Female F2 used a different tree for nesting during the day but was found in the nest tree used by female F3 several times in different nights. Overlap of both females' home ranges was 1% (100% polygons) or 40% (85% activity cores). Home ranges of two tagged males did not overlap, though points of capture were only 50 m apart.

6.4 Discussion

The type of mating system used by a species often determines spacing and size of home ranges (Ostfeld, 1990). In polygynous mammals (Clutton-Brock, 1989), males can occupy large home ranges whereas females maintain small, non-overlapping territories (Ostfeld, 1985). Spacing of females may often depend on food resources (Ostfeld, 1985), but in tree rats with probably specific requirements for nesting, spacing may also be determined by availability of nesting trees. In our study on *T. nigricauda*, home ranges of males in the breeding season were large and overlapped at one study site. We

occasionally observed or captured non-resident males within ranges of tagged males. Male ranges also included home ranges of several females. Female ranges were small and we found no interaction between breeding females. Previous reports on social structure of *Thallomys* include one breeding pair per nest (Smithers, 1971; de Graaff, 1978 and 1981) or groups or colonies (Nel, 1975; Rautenbach, 1982) consisting of members of a family (Roberts, 1951; Stuart and Stuart, 1993), but our results suggest a polygynous mating system.

Activity in both seasons was highest in the early evening, when animals started foraging. Nursing females had a distinctive activity pattern with a second peak just before dawn, probably as females prepared for the long non-foraging period during the day. This pattern presumably reflects the high-energy and water demands of nursing.

Home range sizes of males were larger and those of females were smaller than predicted by the model of Swihart et al. (1988) that shows a general increase of home range size in mammals with body size. According to their formula for herbivorous mammals, the predicted home range size for an average tree rat of 75 g body mass would be 0.86 ha. MCP (90%) of males were 20 -118 times larger than predicted (1-sample t-tests for both seasons: t = 3; d.f. = 4; p = 0.04) and 90% MCPs of females were 3 - 8 times smaller (but insignificantly: t = 0.9; d.f. = 7; p = 0.41). Activity cores of females were 8 - 50 times smaller than predicted (t = -29.5; d.f. = 8; p < 0.001).

Mating system, access to mates, and sex of the individual may be more important than body size in determining home range size. Similarly, the model's prediction was greatly exceeded by actual home range size of flying squirrels (*Pteromys volans)* (Hanski et al., 2000), perhaps due to mode of locomotion of the flying squirrels. Spacing of suitable nesting trees may also influence inter-tree movements of arboreal mammals (Nel, 1975).

Thorns of *Acacia* may effectively protect the tree rats from predators, which may partly explain the species' preference for *Acacia* shrubs. We found that home ranges of adult females were larger in the non-breeding season, although mobility should have been reduced if predation risk would have been higher in shrubs without dense foliage during winter. Furthermore, during the 143 rat-days of our study, no predation was observed. A study on owl pellets in the Kalahari (Nel, 1975) also revealed no evidence of high avian predation on tree rats. Low food availability in the non-breeding season, coupled with independence of females from the nest site at that time, may explain home range sizes rather than predation risk. Furthermore, the subadult females that were not tied to a

nestling litter also had relatively large home ranges in breeding season. Conversely, the small non-breeding home-range size of males may reflect, that larger home ranges in breeding-season were related mainly to reproductive activities.

Large hollow trees, a prerequisite for breeding in tree rats, are abundant in undisturbed savanna landscapes. In large parts of the southern Kalahari, land is agriculturally managed and it is common practice to remove trees for firewood or to gain arable land. These practices raise concern about the conservation status of Kalahari Thornveld savanna woodlands and the associated small mammal fauna.

6.5 Acknowledgments

6.6 References

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Notes on the ecology of the Black Tailed Tree Rat

(*Thallomys nigricauda*)

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Basing on data from a mark-recapture from summer 2002, supplemented by data from previous field sessions, first field data on biological and ecological aspects of the Black Tailed Tree Rat (*Thallomys nigricauda*) are provided. The study presents data regarding sex ratios, population density, mortality rates and reproductive features. By recapturing juvenile tree rats, growth curves could be derived. Curves allowed estimating the onset and progress of reproduction. Animals reach their physiological (potential) maturity with a body mass of about 40 g (about 60 days old). Mating starts in the middle of October, and no litters should be born later than begin of March considering probability of rain and food availability. Mortality is about 0.6 indicating high longevity and a life history towards K-strategy.

Previous observations on the biology of the Black Tailed Tree Rat should be careful revised as the sibling species *T. nigricauda* and *T. paedulcus* might have been mixed up.

7.1 Introduction

The Black Tailed Tree Rat (*Thallomys nigricauda*, Rodentia, Muridae) is a widespread arboreal rodent occurring at the savannahs of southern Africa. Since the middle of the 1980´s, two sibling species are distinguished due to their chromosomal and cranial characters (Gordon 1987; Taylor et al., 1995). At the study site, *T. nigricauda* occurs according to Gordon (1987) and Taylor (pers. comm.). Despite several studies on specific themes like osmo- and thermoregulation as well as on further physiological aspects (Lovegrove et al., 1991; Lovegrove and Heldmaier, 1994; Frean et al., 1998; Haim et al., 2001; Downs et al., 2003), basic biological field data are still missing. The present knowledge derives from occasional observations, mostly from the Kalahari Gemsbok National Park (e.g. Nel, 1975; Nel and Rautenbach, 1975). To understand ecological processes within species and among the small mammal community, profound knowledge on the species considered is necessary. This study provides field data on the biology of *T. nigricauda* obtained from a mark-recapture study.

7.2 Material and Methods

The study was carried out at the Molopo Nature Reserve (S 25° 50´, E 22° 55´; North West Province, Republic of South Africa). The Reserve is situated in the Kalahari Thornveld and covers 240 square kilometres (1000 m a.s.l.). It was used as farmland for cattle breeding since the 1960´s until the middle of the 1980´s.

In summer 2002 a mark-recapture study was carried out at two study sites within the Nature Reserve. Sampling sites, furthermore signed as the study sites A and B, were about 800 metres apart and similar with respect to vegetation. Site A (S 25° 50' 43-55''; E 22° 55' 19-33'') covered 12 hectare; site B (S 25° 50' 16-27''; E 22° 55' 24-39'') was 13 hectare in size. Both sites were considered to be freely accessible for Black Tailed Tree Rats. The study sites covered the area of the home ranges of one (site A), respective two (site B) reproductively active male, including several nesting sites of females (Eccard et al., 2004). Home ranges of additional males might overlap at the study sites.

The mark-recapture study was conducted during the breeding season from January to April 2002. Two foldable live traps (7 x 9 x 23 cm; H. B. Sherman Traps, Inc., Tallahassee) were placed on larger trees either with signs of tree rat use (scats, nests) or if they where supposed to be attractive for tree rats (food or caves). Traps were pre-baited with a mixture of oats, peanut butter and a small amount of jam (de Graaff, 1978) for one night. Trapping happened the following two nights. Traps were set at dusk and checked at dawn while keeping locked during the day. At site A we choose 15 and at site B 14 trees with signs of *T. nigricauda*. Traps were set at intervals of 10 days. To get also data on animals entering the study sites, we set additional traps every 20 days at trees potentially suitable for tree rats (10 at site A; 12 at site B).

Animals caught were sexed, weighted to the nearest gram and marked individually by fur clips at the back. Clips were renewed at the occasion of recapture. Fur clipping is a useful method for marking those animals for a time up to 1 month. The reproductive state of trapped animals was defined by the location of testes in males (active if scrotal; inactive if abdominal) and perforate vulva in females. Sex ratios were computed of sub-adult and adult animals and tested by Log-likelihood tests (G-test with Yates correction for discontinuities, all df = 1). Obvious pregnancy or lactation of females was recorded. Scars at the ears of tree rats caused by tissue sampling enabled us to recognise animals to be caught at least once before. This was relevant to determine whether an individual has been caught in the previous season.

Reproduction

Weaning was estimated by the time span between the first observations of a lactating female und the first capture of its offspring. At nests of nursing females, traps were set at short intervals to detect the first pups outside the nest. Two individuals of each sex were trapped at their first appearance outside and were caught at least once again. The increase of their body masses was used as a reference for ageing further juveniles.

Estimating population size and mortality rates

Population size was estimated by mark-recapture data from summer 2002. Consecutive trap nights were treated as one trapping event. To adequately fulfil the assumption of a closed population, only captures of sub-adults and adults were analysed. We used the program CAPTURE (Otis et al. 1978), which allows testing for equal probabilities of capturing by fitting a set of models to the data. The model applied was chosen by the

model selection criteria as described by Otis et al. (1978). Single trapping events without a save recognition of the individuals were rejected from analyses. Mortality rates were estimated by the MNA (minimum number known to be alive) approach (Krebs, 1999). Analyses were supplemented by trapping data from several sites throughout the Nature Reserve obtained in summer and winter 2001 and summer 2002.

7.3 Results

In a total of 950 trap nights 226 captures were received at the main study sites, yielding 60 individual Black Tailed Tree Rats in summer 2002. Including trapping seasons from summer and winter 2001, the whole dataset consists of about 2500 trap nights with 395 captures and a total of 144 individuals caught.

Body weight

At the study sites A and B mean body mass for females in winter was 65.9 g (SD = 20.5; n = 19; range 38 – 123 g) and for males 77.2 grams (SD = 9.4; n = 6; range 69 – 95). During the summer mean body mass for females was 73.1 grams (SD = 18.1; n = 25; range 46 – 108) and for males 83.6 grams (SD = 14.4; n = 20; range 55 - 106 g). Note, that early states of pregnancy might be kept undetected and could bias the mean body mass in females (one gravid female, yet not included, was 128 grams heavy). Body mass was within the range of animals from Botswana (de Graaff, 1978).

Sex ratios

The sex ratios within sub-adult and adult Black Tailed Tree Rats varied between seasons at the two main study sites as well as between the overall of animals caught at the particular period (Tab. 1). During breeding season in summer 2001 and 2002, more males than females were caught at the study sites, whereas in winter more females were recorded. If including captures from all sampling sites within the Nature Reserve, more females than males were caught. Sex ratios did not significantly deviate from 1:1 (all p > 0.11). The proportion of juveniles (immature) on the total number of individuals caught was 0.43 in summer 2001 (19 out of 44) and 0.42 (33 out of 79) in summer 2002.

Table 1: Sex ratios (m:f) of adult Black Tailed Tree Rats (*T. nigricauda*)at the two main study sites (A and B) and for all sites investigated. Note, that data among the seasons are from a different number of sites.

Season	Site A	Site B	Overall
Summer 2001	1.7:1 (8)	2:1 (6)	0.75:1 (33)
Winter 2001	0.6:1 (13)	0.25:1 (5)	0.4:1 (24)
Summer 2002	1.1:1 (17)	1:1 (26)	0.8:1 (54)

Reproduction

The least weight for potentially mature (reproductively active) *T. nigricauda* was recorded on 40 g body mass both in females (open vulva) and males (testes scrotal). During the winter 2001, the first potentially mature females were recorded at the end of August; two males with descended testes in the second week of September. We found no individual with a body mass below 38 g during winter 2001.

Lactating females were recorded throughout the study with the last observed on the 2nd of April 2002. Time span between the first capture stating them lactating and the first capture of their offspring ranged from 28 to 31 days (n = 5), which is identical to the findings of Meester and Hallett (1970). Thus, we defined juveniles to be 31 days old at the time they moved the first time out of the nest. Yet, we cannot prove that young were fully weaned, but tagged females extended their home ranges remarkably at the same time (Eccard et al., 2004). We thus argue, that offspring depended not any longer on maternal care. Juveniles body mass at time of first capture outside the nest ranged from 16 to 24 g in females (n = 4; mean = 22; SD = 4) and 16 to 22 g in males (n = 4; mean = 19; SD = 2.9). Body masses of seven juvenile females and seven males, respectively were used to estimate growth. Linear regression on the body masses between an age of 31 days and 65 days showed a faster, even not significant (t = 0.54, p > 0.5) increase of body mass in males (fig. 1).
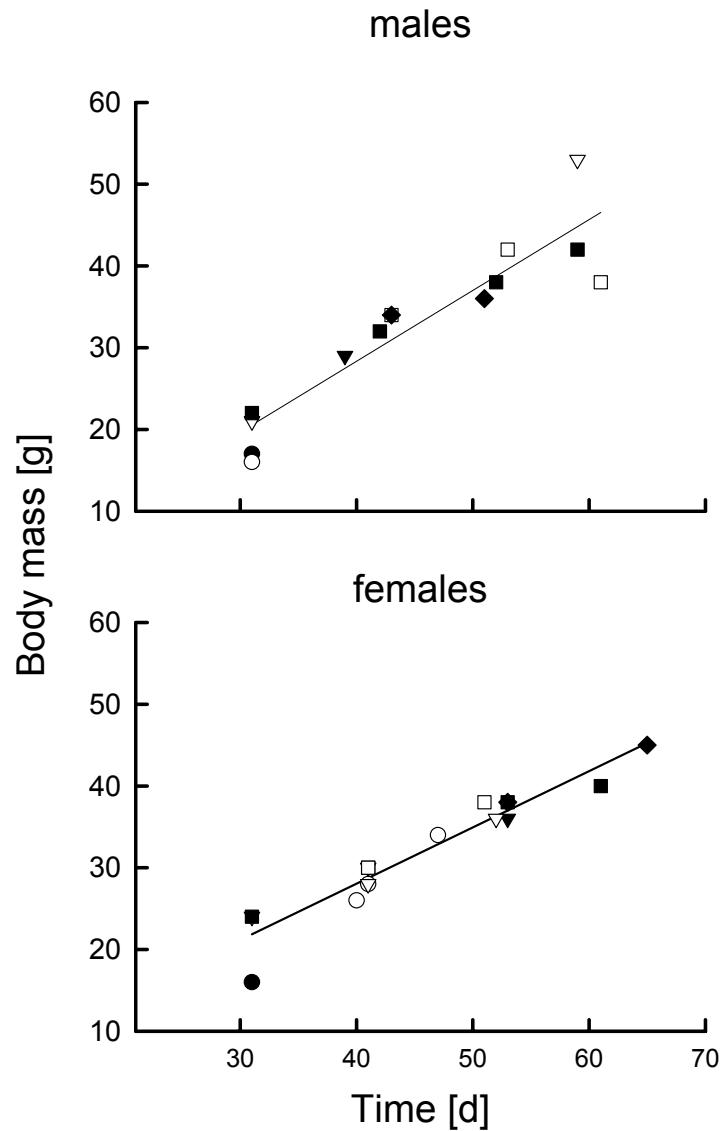
males

Figure 1: Growth curves of juvenile Black Tailed Tree Rats at the Kalahari Thornveld in summer 2002. Capture-recapture data of six animals (symbols) of each sex were used to illustrate growth between age of 31 and about 65 days.

The majority of adult *T. nigricauda* were not yet in breeding condition in the middle of September. Gestation of animals in captive animals is reported to be 26 days (Meester and Hallet, 1970). Because we caught animals weighing about 50 grams in the middle of January, mating must have take place at the middle of October (26 days + 60 days).

Population density

At study site A 85 captures of adults out of 117 were subjected to analyses. At site B data of 65 out of 79 individuals could be used to estimate the population size. The standardised selection criterion for the data from both study sites was highest (1.0) for the model M_h, showing unequal catchability among individuals. Population size was estimated by applying a jackknife estimator (Otis et al., 1978) (Tab. 2). The MNA values and the resulting mortality rates have been calculated for site A only because towards the end of study, no new (= immigrating) individuals of *T. nigricauda* were caught (Tab. 3). Thus, we assume a nearly total record of all animals inhabiting this area.

Table 1: Estimates on the population size of the Black Tailed Tree Rat at two study sites (Molopo Nature Reserve, South Africa) from a capture-recapture study using the model M_h (CAPTURE, Otis et al.; 1978).

Site	Individuals caught		Est. population (95% CL)	Density ha^{-1} (95% CL)
	♂	♀		
A	9	8	19 (18 – 30)	1.5 (1.4 – 2.4)
B	13	13	45 (33 – 74)	3.4 (2.5 – 5.6)

Table 2: Mortality rates in the Black Tailed Tree Rat (*T. nigricauda*) at site A (Molopo Nature Reserve; South Africa; see text) based on MNA data.

Period	nr. caught	nr. From previous period	MNA rate 6 months	mortality rate 1 month	mortality rate 12 months
Summer 2001	8	0	-	-	-
Winter 2001	13	3	0.375	0.075	0.61
Summer 2002	17	5	0.385	0.078	0.62

7.4 Discussion

When discussing our findings, we have to keep in mind, that some of the information gathered from the literature might rely on *T. paedulcus*. Previous results should therefore be carefully inspected if derived either from *T. paedulcus* (De Witt, 1972 cited by Nel, 1975), *T. nigricauda* or if both sibling species became mixed up as probably by Meester and Hallett (1970).

Holding a good trade-off while spending effort if rearing offspring, litter should be born during the time with the highest probability of access to all resources needed for raising young. As in most other animals in areas with pronounced seasonal rain distribution, reproduction of *T. nigricauda* is linked to the availability of water-rich food (Meester and Hallett, 1970; de Graaff, 1978; Frean et al., 1998). Months with highest predictability of rain at the study area range from October until March (see chapter 3: fig. 3). In April rain may fall in sufficient amounts, but on average, every three years the April keeps dry (< 10 mm rain). Therefore, the April is supposed unsuitable for giving birth. Considering the body mass of individuals caught in winter, we suggest a body weight of about 40 grams (= maturity) necessary to survive the winter. Thus, litters should be born not later than begin of March, enabling pups to reach this body weight.

Meester and Hallet (1970) observed, that females gave birth to their first litter not before they are about 107 days old. We are not able to falsify this observation, but as we can show, *T. nigricauda* becomes mature at a body mass of about 40 grams, which they gain at an age of 50 – 60 days. First litter could be born when the female is about 80 to 90 days old. There is no reason, why they should stay in a non-reproductive state as long physiological and nutritional requirements are fulfilled. Furthermore, a female of 54 grams body mass, who accidentally died while handling, carried three well-developed embryos. Perhaps, a limiting factor for reproduction could be the availability of nest suitable for giving birth and raising offspring (Meyer et al., 2004). Females born early become physiologically able to reproduce by themselves within the same breeding season.

Different environmental conditions may have led to differentiated responses regarding population parameters and behavioural aspects. Observations from the Kalahari Gembsbok National Park implied that *T. nigricauda* lives in small colonies or family groups (Nel, 1975; Nowak ed., 1991; Apps, 2000). We always found only females with their offspring living temporarily together. In winter we observed one nest inhabited by an adult female (known from the previous summer) and two subadult females, probably her daughters.

The densities found at the study sites must be considered high, due to the good habitat quality of the study sites (Meyer, 2004). An effect on the density estimates may have had the boundary effects. Partly overlapping home ranges of individuals, namely males, around the study sites could cause an over-estimation of the local density. If the core area of activity is small in relation to the area studied, those "boundary-effect" can be

neglected. Thus, the small home ranges of females (Eccard et al., 2004) should certainly have not caused biased estimations, but those of males might have. This becomes underlined because the sex ratios in adults at the main study sites were male-biased during breeding season, but not at the non-breeding period. The male-biased sex ratios at the study sites can be explained by a considerable number of nesting trees inhabited by females at these particular sites. Whereas number of females kept approximately constant due to restricted numbers of suitable nests available, several males might have entered the study sites while searching for mates. In general we suggest a female-biased sex ratio in adult Black Tailed Tree Rats.

Mortality rates allow for a maximum life span of about 4 years reported from captive animals (Jones, 1982). The high potential longevity, small burst sizes and low mortality combined with a year-round good availability of food (Meyer et al, submit.) make strong population cycles, dependent by population density and climate, less likely (Nel, 1975). Mortality seems depend on terrestrial rather than to aerial predation (Nel, 1975). Within 80 pellets of a barn owl collected at study site A, we found only one fragment suspected to belong to *T. nigricauda*. Although this study gave first insights into the biology of *T. nigricauda*, there are a couple of questions left. A large-scale comparison of landscape structure and ecological features within arboreal rodents seems a basic need for giving recommendations for sustainable management.

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Diet of the arboreal Black Tailed Tree Rat

(*Thallomys nigricauda*)

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The arboreal Black Tailed Tree Rat (*Thallomys nigricauda*) has been reported to feed on *Acacia* leaves and buds. To assess the impact of increasing densities of *Acacia* shrubs due to human use of savannah ecosystems (shrub encroachment), a diet analysis was carried out. Scats were collected in summer and winter at nests of *T. nigricauda* (Molopo Nature Reserve, South Africa). Leave characters allowed for species determination in 53.8% (4009) of fragments. Leaves of *Acacia mellifera* and *A. luederitzii* comprised about 95 % of the diet, more than their relative abundance at the certain study sites. The same preference was found in winter, although both *Acacia* shrubs offer only dry leaves at that season. The total number of different items taken was larger in winter than during summer. Insects were taken throughout the year at small proportions. A strong dominance of either *A. mellifera* or *A. luederitzii* fragments within the samples was found, but this did not necessarily reflect their dominance at the particular habitats. Individual preferences as well as the distance between nest and food plant could cause this effect. It is concluded, that the process of shrub encroachment improves the food availability for the Black Tailed Tree Rat.

8.1 Introduction

The savannahs of Southern Africa are widely used for commercial farming of domestic stock and / or antelopes. Selective grazing increases the abundance of woody plants ("shrub encroachment"), which may have considerable effects on native mammals (Jeltsch et al., 1997). However, we have still limited knowledge on the niche requirements of many species, even mammals and their response to habitat changes. Here we report on the diet of the arboreal Black Tailed Tree Rat (*Thallomys nigricauda*; for taxonomic issues see Gordon, 1987 and Taylor et al., 1995) to predict the impact of shrub encroachment on the resource situation for this rodent. Although the arboreal Black Tailed Tree Rat is widespread and common in southern Africa, little information on the biology is available (Rautenbach, 1971; Nel and Rautenbach, 1975; Rautenbach and Nel, 1975; Skinner and Smithers, 1990). There is circumstantial evidence that the tree rat consumes leafs of trees and shrub encroachment might increase food availability for this species.

8.2 Material and Methods

The study was conducted at the Molopo Nature Reserve (Republic of South Africa; S 25° 50´; E 22° 55´). Rain (mean 320 mm) allows for an open woodland savannah dominated by *Acacia erioloba*, *Boscia albitrunca* and *Terminalia sericea* as well as by the shrubs *Acacia luederitzii*, *A. mellifera*, *Grewia flava* and *Ziziphus mucronata*.

Fresh scats were collected at nests of the Black Tailed Tree Rat within eight study sites along a 30 km transect across the reserve. Most study sites were 9 to 10 hectares in size, which is the home range size of reproductive males (Eccard et al., 2004). Two sites had an area of 0.2 and 0.5 ha. In 2001 and 2002 five samples (> 20 scats) were collected at four sites in summer (February to April) and sixteen samples at the other four sites during winter (August to September) and dried. Three scats were randomly selected from each sample, soaked with water until they were soft, stirred and sieved to select diet fragments between 0.25 mm and 1 mm. Fragments were dehydrated with absolute ethanol for five minutes and mounted on slides (for details see McAllister and Bornmann, 1972). Fragment characters were compared with a reference collection

(magnification 250x). Distinct leaf characters (trichomes, stomata and cell-shape) allowed identification to species. On hectare plots (one to seven per site; except at the two small sites, which were completely surveyed) all plants of at least 1 m were recorded. Abundances are given per hectare. Prior analyses, data were weighted according to the particular number of plots surveyed per site and the number of samples taken there. The use of items for food, movement and nesting relative to their presence in the habitat was compared by G-test (Krebs, 1999). Food preference was estimated by the standardized selection index B_i (Manly et al., 1993, Krebs, 1999). B_i values of (1 / number of resources) indicates food intake according to the availability (= no selection). Values above this indicate a relative preference, values below relative avoidance.

Table 1: Percentages of food items in scats of *Thallomys nigricauda* across all samples (n = 21) and standardized selection index B_i, ± 95% CL (Manly et al., 1993; Krebs, 1999), percentages within samples from summer (n = 5) and winter (n = 16) and C/N ratios of food plants. Numbers of fragments are given in parentheses.

Diet	Total %	Total B_i ± 95% CL	Summer %	Winter %	C / N ratio
Common items					
Acacia mellifera	48.7 (2064)	0.39 ± 0.16	62.3 (727)	47.0 (1337)	14.3
Acacia luederitzii	47.8 (1848)	0.38 ± 0.16	37.7 (442)	49.1 (1406)	20
Boscia albitrunca	2.0 (50)	0.06 ± 0.27	0	2.2 (50)	14.3
Rare items					
Grewia flava	0.07 (3)	0.00 ± 0.04	0	0.1 (3)	20
Dichrostachys cinerea	0.78 (25)	0.05 ± 0.52	0	0.9 (25)	20
Terminalia sericea	0.5 (19)	0.64 ± 1.89	0	0.7 (19)	25
Acacia erioloba	0	0	0	0	20
Ziziphus mucronata	0	0	0	0	16.6

8.3 Results and Discussion

From 7456 fragments 4009 (53.8%) could be identified to species. This ratio is comparable to other studies on the diet of small mammals (Kerley, 1989; Gaylard and Kerley, 1997). The total number of items taken is larger during winter than during summer (Tab. 1). Insects were taken at small proportions (0.8% of fragments from summer-scats, n = 10 and 4.4%, n = 130 in winter) throughout the year. Frequencies of plant species in the scats differed from their relative abundance across all sites ($\chi^2 = 492$; df = 7; p < 0.0001) as well as from the usage during foraging ($\chi^2 = 33$; df = 5; p < 0.0001) and nesting ($\chi^2 = 122$; df = 5; p < 0.0001; fig. 1).

Nesting sites of the tree rat were almost exclusively located in caves and crevices of non-food trees (96%, fig. 1). Results indicate a clear preference for *A. mellifera* and *A. luederitzii* as food. For individual sites one finds either a clear preference for *A. mellifera* or for *A. luederitzii*, irrespectively of the abundance at that particular site (Tab. 2). This may be due to individual preferences as well as spatial arrangement of shrubs.
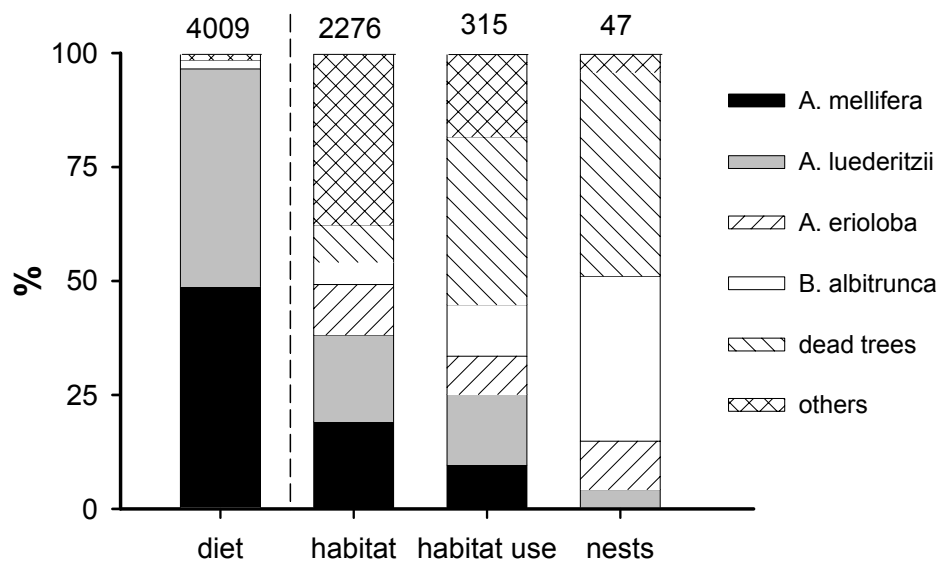

Figure 1: Relative abundances of woody plant species observed within the diet of *Thallomys nigricauda* (n = identified fragments), across all sites (n = number counted), habitat use (n = number of locations) and nesting sites (n = number of nests). Diet does not include the category "dead trees".

The shrubs *A. mellifera* as well as *A. luederitzii* have dry leaves in winter, whereas the trees *A. erioloba* and *B. albitrunca* offer green foliage throughout the year.

Nevertheless, the utilization of those two plant groups did not differ between summer and winter (χ^2 = 1.42; df = 1; p = 0.23; Tab. 1). But note, that we sampled different sites during summer and winter. Nel (1975) and de Graaff (1978) reported Black Tailed Tree Rat feeding on pods, bark and leafs of *A. erioloba* and leaflets of *Z. mucronata*. We were not able to confirm this. We observed tree rats feeding on pods of *A. luederitzii*. Pods and fleshy fruits (the latter are exclusively available in summer) may be underrepresented in our analysis, as pods and fruits have few characteristics for identification. But, if fruits were a substantial proportion of the diet, one would expect an increase of unidentifiable fragments during summer. However, this was not the case (χ^2 = 0.002; df = 1; p > 0.9).

Reasons for the food preferences in the Black Tailed Tree Rat could be the palatability of the selected food (Downs et al., 2003) as well as protection by the thorny shrubs during foraging. Preliminary analyses of C and N contents of leaves provided little evidence for differences in the C/N ratio between the species (Tab. 1). Hence, the Black Tailed Tree Rat needs two key resources within the home range: trees for nesting and certain shrub species for food. At the Thornveld savannah, both main food shrubs are the major encroachers (Totlolo, 2003). Thus, our results suggest that the increase of the abundance of *A. mellifera* and *A. luederitzii* improves food resources for the Black Tailed Tree Rat.

8.4 Acknowledgments

Table 2: Standardised selection indices B; of the food categories *A. mellifera*, *A. luederitzii* (both with ± 95% CL) and all other items (pooled) at sampling sites during summer and winter (sites numbered I to VIII; values in parentheses: number of scat samples; area surveyed in ha) and both seasons together. Mean densities of *A. mellifera* and *A. luederitzii* (weighted means for "overall" columns) are shown.

Site (scats; plots)	Summer				Winter				Overall		
	I (1;1)	II (2;2)	III (1;0.2)	IV (1;4)	V (4;7)	VI (5;3)	VII (4;2)	VIII (3;0.5)	Summer (5; 7.2)	Winter (16;12.5)	Total (21;19.7)
Acacia mellifera	0.04 ±0.04	0.07 ±0.01	0.88 ±0.01	1 ±0.01	0.80 ±0.02	0.06 ±0.07	0.93 ±0.03	0.56 ±0.1	0.29 ±0.02	0.53 ±0.04	0.50 ±0.03
Acacia luederitzii	0.96 ±0.01	0.93 ±0.01	0.12 ±0.01	0	0.2 ±0.05	0.92 ±0.01	0.56 ±0.03	0.42 ±0.04	0.71 ±0.03	0.45 ±0.03	0.49 ±0.03
Others	0	0	0	0	0.01	0.02	0.04	0.02	0	0.02	0.01
<u>Density</u>											
A. mellifera ha-1	12	68	1	8	20	29	29	142	57	110	90
A. luederitzii ha-1	4	3	5	5	27	16	7	708	14	134	90

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Vegetation structure and the abundance of the Black Tailed Tree Rat *Thallomys nigricauda* at the Thornveld savannah (South Africa)

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The use of semi-arid savannahs often causes an increase of thorny shrubs due to selective grazing of domestic stock. At the study site (Kalahari Thornveld, South Africa) especially *Acacia mellifera* and *A. luederitzii* contribute to the encroachment process. The elevation of potentially connecting structures between single, large trees is assumed to improve habitat conditions for the arboreal Black Tailed Tree Rat (*Thallomys nigricauda*). Habitat requirements were analysed on the grain of home ranges for males (about 10 ha) and nursing females (0.01 – 0.03 ha). Relative tree rat abundances were expressed as numbers of nests and scats per hectare. Relative abundance of tree rats at the grain of male home ranges was determined by the presence of large, live trees (> 5m), especially *Boscia albitrunca* and food plants (*Acacia mellifera* and *A. luederitzii*; >1 m – 3 m). Their lowest, perhaps limiting density was estimated on one tree and about 10 food plants per hectare at least. Trees harbouring a nest were found to have always at least one food plant within a 15 m distance; nesting trees used for rearing offspring must provide food within the immediate surrounding (patch). As this constellation is rare at the study site, nesting trees suitable for raising offspring might become a limiting factor for the viability of the population. Large dead trees provide frequently caves and hollows for nesting, but they cannot reliable be used for predicting permanent tree rat occurrence if no food plant stand within a short distance. The increase of *Acacia* shrubs improves habitat conditions for the Black Tailed Tree Rat, as long nesting facilities keep available.

9.1 Introduction

Savannahs are characterised by the patchy presence of trees and shrubs within a grassy matrix (Delany and Happold, 1979; Jeltsch et al., 2000). Due to the lack of a closed woody cover, savannahs have no high complexity in terms of several height strata (August, 1983). Consequently, arboreal animals are considerably isolated to the next suitable habitat. If semi-arid savannahs become used for breeding cattle, the grazing pressure increases; giving woody plants an advantage over grass (van Langevelde et al., 2003). At the same time, prevention of bush fires fastens this process called the "shrub encroachment". The arising shrub layer is assumed to improve connection between trees for arboreal animals.

The habitat requirements of arboreal mammals as well as the impact of changing parameters regarding structural composition have been investigated in boreal and tropical zones (Henderson et al., 1985; Wauters et al., 1994; Shepherd and Swihart, 1995; Lindenmayer et al., 1999; Hanski et al., 2000; Capizzi et al., 2003). But, those studies usually focused on the fragmentation of habitats rather than a possibly improved connectivity.

The murid rodent *Thallomys nigricauda* (Black Tailed Tree Rat) is a widespread arboreal rodent in the dry savannahs of southern Africa. It inhabits caves within larger trees and is occasional reported to build twig nests in hollows and forks (Shortridge, 1934; Nel, 1975). The food consists mainly of leaves of *Acacia mellifera* and *A. luederitzii*, which are the major encroacher plants at the study area (Meyer et al., submit.). Home ranges of reproductive active males are up to 10 ha (Eccard et al., 2004). The scattered distribution of shrubs and trees in the savannah allows not for moving across such large home ranges without even touching the ground. Therefore, more shrubs between trees should made movements safer.

Home ranges of nursing females were found to be much smaller (up to 0.03 ha). Those small home ranges would allow for higher densities of nursing females than observed. We found several trees, which were, in our opinion, suitable for nesting, but were not used for raising offspring in breeding seasons 2001 and 2002. We therefore asked, if nests and their surrounding must fulfill specific requirements to become used for rearing offspring. Alternatively, the number of nursing females per hectare could be, however, density-depend regulated.

We hypothesized that i) an increase of shrub density improves the habitat quality for *T. nigricauda* regarding connectivity and availability of food; and ii) nesting sites of nursing females may differ from other large trees regarding nest parameters or food availability.

9.2 Material and methods

Study area

The study was conducted at the Molopo Nature Reserve (S 25° 50´; E 22° 55´; Republic of South Africa, fig. 1). The reserve is situated in the semiarid part (about 1000 m a.s.l., mean annual rain = 320 mm) of the Kalahari. Since the 1960´s this part of the Kalahari became used for cattle breeding. The reserve itself was used as farmland until the middle of the 1980´s. With the exception of occasional burning of grassy blocks, no management influences the ecosystem.

The study area belongs to the Kalahari Thornveld (Acocks, 1988). The dominating trees are *Boscia albitrunca* (Shepherd Tree), *Acacia erioloba* (Camelthorn) and some individuals of *Terminalia sericea* (Silver Cluster Leaf). The most abundant shrubs are *Acacia mellifera* (Black Thorn), *A. luederitzii* (False Umbrella Thorn), *Grewia flava* (Raisin Bush) and *Dichrostachys cinerea* (Sickle Bush). Additional shrubs are *Ziziphus mucronata* (Buffalo Thorn) and, rarely, *Grewia retinervis* and *Acacia hebeclada* (Candlethorn).

Data sampling and analysis

Data were collected during summer and winter 2001 and summer 2002 on study sites (n = 15) along a 30 km transect across the reserve and at three farmlands. Hence, sites were at least 0.8 km distant to each other, they were not isolated and considered potentially accessible for *T. nigricauda*. Sites were chosen due to the presence of large live and dead trees, which were considered to be determinants of tree rat occurrence (Nel, 1975; de Graaff, 1978; Nowak, 1991).

Indirect estimates of abundances are used in species living cryptic, wide roaming or sensitive to disturbances (e.g. Navaro et al., 2000; Predavec et al., 2001; Tuyttens et al., 2001). Relative abundances are given in relation to distinct signs of the certain species (e.g. density of tracks, scats, occupied dens). We defined the number of nests and accumulations of scats (minimum 10 scats) found distant from nests (> 50 m, twice the

diameter of female home range) per hectare as "relative tree rat abundance". Male tree rats often use inconspicuous day hides, thus the record of a larger amount of scats is considered an equal informative feature of inhabitancy of an area. Appearance of faeces allowed safe distinction from scats of the arboreal Savannah Dormouse (*Graphiurus sp.*), the Namaqua Rock Mouse (*Aethomys namaquensis*), which sometimes enters shrubs and trees as well from lizard scats. Permanently marked scats of *T. nigricauda* remained not longer than 1 year in the field (Meyer, pers. obs.), therefore counts of nests and scats are supposed to be at one temporal scale like the records on the habitat variables.
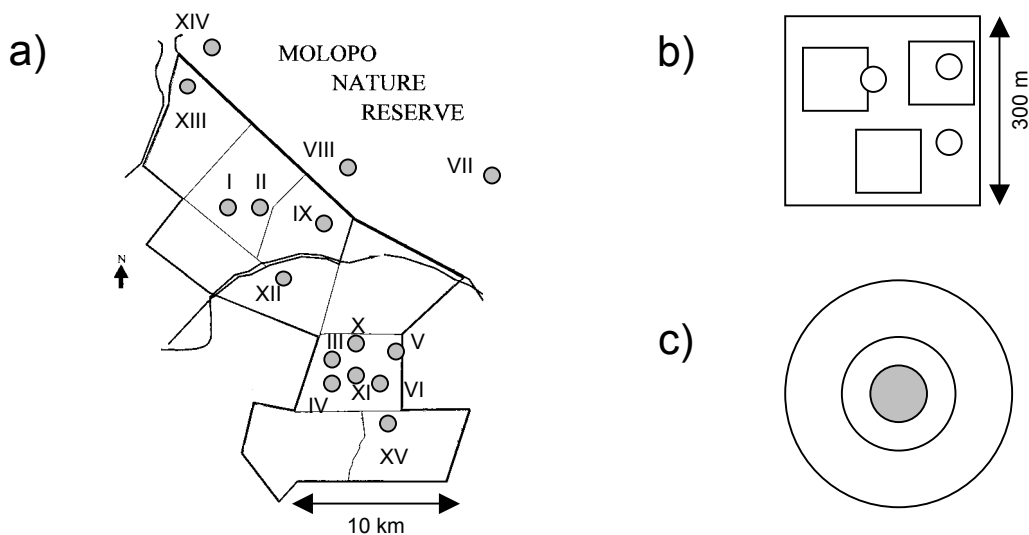
Figure 1: Map of a) the Molopo Nature Reserve (North-West-Province, South Africa) and the distribution of study sites (circles) within. Increasing roman numbers sign study sites according to the relative abundance of the Black Tailed Tree Rat (high numbers = high abundances, see Tab. 1). Plate b) illustrates a possible pattern of hectare plots (rectangles) and nesting sites (open circles), the latter were surveyed at three distances around the nesting tree c) the patch (grey circle) and distances of 15 m (second circle) and 30 m (outer circle).

Woody plants were recorded at plots of 100 by 100m and assigned to size classes (>1 to 3 m; >3 to 5 m and >5 m). Shrubs below 1 m are not used by *T. nigricauda* (Eccard et al., 2004). Number of plants were averaged across plots and expressed as density of individuals per height class (Tab. 1). Grass cover of annual and perennial grass was estimated at each plot and averaged per site. The dependence of the abundance of *T. nigricauda* from single habitat variables to was analysed by linear regression. Prior to regression analyses, data were square root transformed (Zar, 1999).

To reduce the number of variables, data from vegetation records were subjected to groups, which we supposed to have similar importance for the tree rat:

1. FOOD SHRUBS: all individuals of *Acacia mellifera* and *A. luederitzii* larger than 1 m as the dominant food plants (Meyer et al., submitted.).
2. NON-FOOD SHRUBS: all other shrubs between >1 and 5 m height.
3. LARGE TREES: all live trees larger than 5 m. Nests and day hides found were mostly located within such large trees (Tab. 1). Alive trees, especially *B. albitrunca* and *A. erioloba* are usually not removed as they provide shade and green leaves as protein rich nutrition for domestic stock throughout the year.
4. DEAD LARGE TREES: they provide nesting facilities for tree rats (Tab. 2), but are preferably removed for firewood.
5. COVER: the total area covered by shrubs and trees, if projecting them vertically down to the ground.

Variables were subjected to a hierarchical partitioning analysis using the free software "R". This method allows estimating for the specific relevance of each independent variable by partitioning their variances. During this procedure the certain variable under consideration is added to each possible combination of the remaining variables (to all first-order models up to the (n-1)th-order models). The relative increase of each goodness-of-fit test is used to give a measure of the relative, independent meaning of each variable. Thus, variation caused by a single variable and variations shared with other independent parameters become assessable. The independent partitions of each variable were tested for their significance by bootstrapping (Manly et al., 1997). Hierarchical partitioning overcomes shortcomings due to multicollinearity or antagonistic coactions among independent variables (Chevan and Sutherland, 1981; MacNally, 1996 and 2000).

Nesting sites

Data on nests of *T. nigricauda* were obtained on its harbouring structure (species, height class, living / dead) and the vegetation patch around. According to the observed use for rearing offspring, nests were categorised into:

   category A: occupied for a short time, by the same or different animals (temporarily used); or

category B: offspring raised in at least one summer (2001 and / or 2002).

Random coordinates were generated for 10 sites inhabited by *T. nigricauda*. Large tree standing next to the particular coordinate became measured if no signs of Black Tailed Tree Rats were found. Vegetation around nests and random trees was rinspected at three distances: the patch (13 to 75 m^2) and circles of 15 m (706.5 m^2) and 30 m (2826 m^2) radius, respectively. A patch was defined as the central tree and all under-storey plants. The stepwise extension of plant records (patch, 15 m and 30 m) included all plants of the previous distances. We compared the number of trees with at least one food plant in the patch and / or 15 m respectively 30 m radius by 2x2 contingency tests.

Table 1: Sampling sites, densities of Black Tailed Tree Rat abundance and the main habitat variables [ha^{-1}] (see text for description).

Site	Tree rat abundance	Live trees > 5 m	Dead trees > 5 m	Food plants > 1–5 m	Non-food >1–5 m	Woody cover %	No. plots	Size ha
I	0.00	1.5	1.0	11.0	31.5	8.3	3	1.4
II	0.00	0.0	0.7	3.6	5.7	2.0	1	1.1
III	0.00	5.2	0.0	1.7	27.0	6.8	1	1.4
IV	0.08	3.0	1.5	2.0	28.0	9.1	5	11.8
V	0.14	1.0	2.0	29.7	18.3	8.1	6	21
VI	0.17	0.0	0.0	13.3	27.3	5.5	4	24.2
VII	0.24	2.3	0.3	37.3	15.3	9.8	4	8.3
VIII	0.37	1.3	3.0	20.0	6.5	5.7	4	8.1
IX	0.47	1.3	2.7	12.0	16.7	7.0	3	4.2
X	0.90	1.0	0.6	45.5	12.3	8.8	8	13.3
XI	0.97	4.0	1.7	44.7	22.3	11.4	4	12.4
XII	1.33	2.5	1.5	70.0	29.0	11.3	3	3
XIII	1.38	4.0	1.5	34.4	25.0	10.0	9	13.8
XIV	1.47	5.5	0.5	20.0	36.0	9.8	3	6.8
XV	1.93	7.0	1.0	14.6	11.1	6.9	3	8.8

9.3 Results

Tree rat abundance was significantly correlated (pair-wise correlations) to the density of *A. mellifera* (>1 − 3 m, r^2 = 0.59, p < 0.001) and large *B. albitrunca* (>5 m, r^2 = 0.37, p = 0.02). The density of small (>1 - 3 m) and large trees (>5 m) of *A. erioloba* and the shrub *A. mellifera* (>5 m) were marginally significant related (all p < 0.1). Abundances

of *T. nigricauda* were not correlated to total grass coverage ($r^2 = -0.22$, p = 0.11) and only marginally significant to annual plants ($r_S^2 = 0.26$, p = 0.07) as well as to perennial grass coverage ($r^2 = -0.28$, p = 0.06).

Hierarchical Partitioning

Results from the hierarchical partitioning analysis shows the presence of large, live trees and the shrubs (1-3 m height) of *A. mellifera* and *A. luederitzii* as the determining habitat parameters for the occurrence of *T. nigricauda* (fig. 2). Their independent partitions explain for a significant amount of the variance within the data. Large, dead trees do not provide any significant contribution for variance explanation.
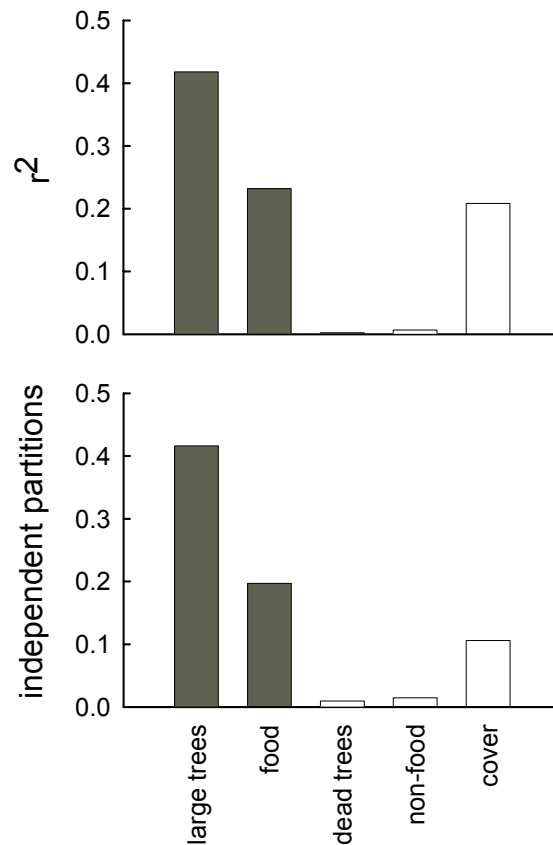
Figure 2: Hierarchical partitioning analysis on structural variables on the abundance of the Black Tailed Tree Rat at 15 sampling sites (Molopo Nature Reserve, South Africa). Plate a) gives the overall r^2 values for all 2^S regression models; plate b) presents the independent partitions analysed by bootstrapping (Manly et al., 1997). Black bars shows significance (large trees: p = 0.04; food plants: p = 0.05).

Among the grouped habitat variables, both *Acacia* shrubs (food) show a high contribution to the total coverage ($r^2 = 0.46$; p < 0.01, sequential Bonferroni corrected).

Indeed, the mean density of *A. mellifera* shrubs (>1 to 3 m high) was 18.3 ha^{-1}, SD = 9.65), while abundances of each other non-food plant were below 5.2 ha^{-1}. To get an estimate on the limiting densities of large trees and food plants, their relationship between one another was inspected. Both habitat features are significantly positive related to tree rat abundance (both r^2 > 0.3; p < 0.05), whereas both parameters can be considered independent among each other (r^2 < 0.005; p = 0.79). The lowest density of live large trees should be approximately one tree per hectare (fig. 3), but might be lower if smaller (<5m) suitable trees are available (see Tab. 1). The minimal density of suitable food plants should be about 10 plants ha^{-1}. This assumption is strongly supported by a modelling study done at the same study area (Steinhauser, 2004).

Fig. 3: Three-dimensional relationship of the key habitat variables large trees and food plants on the abundance of the Black Tailed Tree Rat (r^2 = 0.58, F$_{2,15}$ = 10.5, p = 0.002). Filled dots show site with relative tree rat abundances above 0.1; triangles such of < 0.1. Data are square root transformed.

Nest site selection

A total of 47 nests were recorded. Thirty-six (74.5%) nests were found within trees larger than 5 m, eleven (23.4%) in trees between >3 and 5 m and only one nest (2.1%) was localised inside a 3 m high stem of a *B. albitrunca*. Large live trees of *B. albitrunca* and large dead trees are the preferred nesting sites, whereas large individuals of *A. erioloba* were used equivalent to their occurrence (Tab. 2).

Table 2: Number and percentages of nests of *Thallomys nigricauda* found in different structures at the study area compared with their potential availability. Asterisks indicate significant 2x2 contingency test: * = p< 0.05; ** < 0.005 and *** <0.0005.

	Nests		Habitat	
	n	%	n	%
A. erioloba				
3 –5m	1	2.1**	285	39.5
> 5m	4	8.5	58	8.0
B. albitrunca				
3 – 5m	2	4.3	61	8.5
>5m	14	29.8***	25	3.5
Dead trees				
3 – 5m	7	14.9	152	21.1
> 5m	14	29.8*	90	12.5
Others				
3 - 5m	2	4.3	24	3.3
> 5m	3	6.4	26	3.6
Sum	47	100	721	100

Nest type analysis

Vegetation was recorded around 21 (mean diameter = 45.9 cm, SD = 16.3) nesting trees with no offspring (category A), 15 nest trees with offspring reared within (category B; diameter = 36.7 cm, SD = 15.2) and 15 reference trees (diameter = 38.7 cm, SD = 11.6). Around nests with offspring, more frequently food plants were standing within the patch (G > 8.8, p < 0.01) than in the other both tree categories (fig. 4).
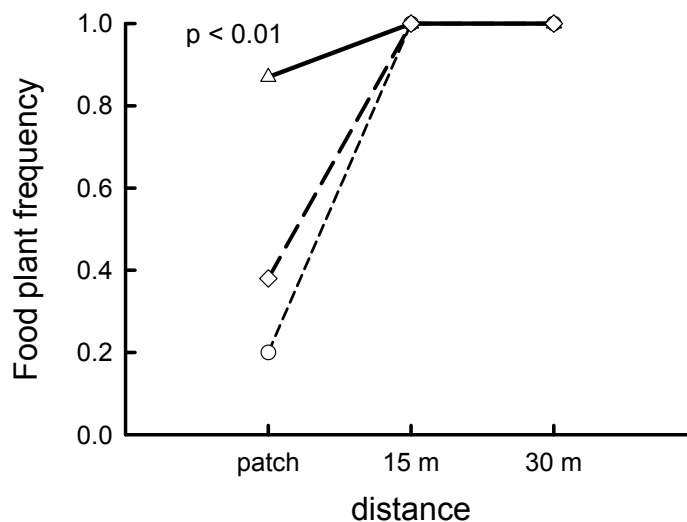
Figure 4: Frequency of food plants present within the patch and circles of 15 m and 30 m radius around nest trees. Solid line: nests with offspring reared; bold dashed line: nest without offspring observed and thin dashed line: random large trees.

There was no difference among all nest categories regarding non-food plants at all distances (all p > 0.17). The number of large trees at a particular site having 25 cm stem diameter and more (n = 158) were compared with that proportion, which had food plants within their patches (n = 45). Sites with tree rat abundance values below 0.1 were excluded. Food plants were present within 36% of patches of *B. albitrunca*, 30% of dead *A. erioloba* and 21% of live *A. erioloba*. Food plants and large trees were not associated (χ^2 = 83.4; df = 10; p < 0.0001).

9.4 Discussion

The increase of both *A. mellifera* and *A. luederitzii* elevates the connecting stratum within the landscape from ground level up to a height between 1 and 5 m, potentially enabling an arboreal animal to move larger distances inside the save thorny cover. This process becomes especially pronounced if shrubs form thickets. As the *Acacia* shrubs are the dominant encroacher, the improved availability of food is considered subsidiary. Tree rats do not deplete even single, larger *Acacia* shrubs within at least several weeks (Meyer et al., submitt.). Thus, the total amount of food present exceeds the amount necessary for maintaining the animals occurring there. If shrub density increases, the probability of food shrubs standing close to potential nesting trees will also increase and built up connections between inhabited areas and formerly spatially isolated larger trees. An increasing shrub cover reduces the extent of the grass layer, both of perennial and annual ones. But, the abundance of *T. nigricauda* was positive correlated to the presence of annual plants, which are a sign of disturbances within natural vegetation assemblage, and is absent in years with low rainfall. The negative correlation to perennial grass cover must be considered as an effect of multicollinearity, because *T. nigricauda* responds positively to shrub density, which in turn suppresses perennial grass cover. Consequently, *T. nigricauda* seems not to depend on a certain degree of grassy cover; even they frequently move 20 m and more on the ground. Zollner and Lima (1997) found a ground dwelling small rodent (*Peromyscus leucopus*) able to detect its favourable habitat (forest) at a maximum distance of 20 m. The arboreal Black Tailed Tree Rats is probably able to recognise adjacent stands of shrubs and trees on

larger distances. We still do not know if the decision of moving towards neighbouring structures depends also on the grass cover between or just on the distance to go.

From a study in the Transvaal bushveld on *Thallomys paedulcus* de Witt (1972, cited by Nel 1975) argued that an increase of ground cover leads to a higher ground and inter-tree movement. As a consequence, the social grouping might become looser. We suggest, that the amount of suitable nesting trees at the study area is higher than at the Kalahari Gemsbok National Park and consequently a wider spatial distribution of animals is possible. Several sources reported the use and inhabitancy of twig nest by the Black Tailed Tree Rat (Nowak ed., 1991; de Graaff, 1978; Nel and Rautenbach, 1975; Skinner and Smithers, 1990). We found only three such twig nests within the whole study area. In agreement with de Graaff (1978), we argue that such structures are used only occasionally. If twig nests would provide an alternative nesting strategy, one could expect them at areas were food supply is present but larger trees are lacking or still occupied.

Regarding the extracted key habitat variables and the preferred nesting places, a discrepancy appears to happen. Large dead trees are frequently used for nesting due to the chance of hollows in it. But, their lonely presence cannot *vice versa* be used as a criterion for habitat quality. Only their combination with food shrubs close to it (< 15 m) provides a suitable nesting facility. Trees providing both hollows and food within the patch are a scarce resource in the Thornveld savannah. We therefore suggest them a limiting parameter for both, the density of nursing females and probably for viable populations. The scarcity of suitable nesting sites strongly implies a directed search of pregnant females for such places. Nest selection by pregnant females aims on a small home range necessary as long as pups are nursed. One reason could be the defence of offspring against enemies. Even nursing females behave very aggressive when caught and being handled, it seems questionable that they are able to defend their offspring against predators like owls, cats and snakes. But they may successfully do so against male tree rats, even still nothing is known about possible infanticide in tree rats. Minimizing energy expenditure and water loss to ensure sufficient lactation could be an additional explanation.

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10.1 Acknowledgements

10.2 Erklärung zur selbständigen Anfertigung der Arbeit

Ich versichere hiermit, daß ich meine Dissertation

The impact of habitat structures on some small rodents in the Kalahari Thornveld

(South Africa)

selbständig, ohne unerlaubte Hilfe angefertigt und mich keiner anderen als der von mir ausdrücklich bezeichneten Quellen und Hilfen bedient habe.

Die Dissertation wurde in der jetzigen oder einer ähnlichen Form bei keiner anderen Hochschule vorgelegt und hat keinen sonstigen Prüfungszwecken gedient.

Marburg, den 30.03.2004

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