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THE COMPARATIVE ECOLOGY OF TWO SMALL MAMMAL COMMUNITIES IN THE KRUGER NATIONAL PARK

by

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Submitted in partial fulfillment of the
requirements for the degree of

M.Sc. (Zoology)

in the
Faculty of Science
University of Pretoria
Pretoria

JUNE 1987

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Pouched Mouse (Saccostomus campestris)

TO A FIELD MOUSE

Wee, sleekit, cow'rin, tim'rous beastie,
O what a panic's in thy breastie!
Thou need na start awa sae hasty,
Wi'bickering brattle!
I wad be laith to rin and chase thee
Wi' murd'ring pattle!

I'm truly sorry man's dominion
Has broken nature's social union,
An' justifies that ill opinion
Which makes thee startle
At me, thy poor earth-born companion,
An' fellow-mortal!

I doubt na, whyles, but thou may thieve;
What then? poor beastie, thou maun live!
A daimen icker in a thave
'S a sma' request:
I'll get a blessin' wi' the lave,
And never miss't!

Thy wee bit housie, too, in ruin!
Its silly wa's the win's are strewin':
And naething, now, to big a new ane,
O' foggage green!
And bleak December's winds ensuin'
Baith snell an' keen!

Thou saw the fields laid bare and waste
And weary winter comin' fast,
And cozie here, beneath the blast,
Thou thought to dwell,
Till, crash! the cruel coulter past
Out thro' thy cell

That wee bit heap o' leaves an stibble
Has cost thee mony a weary nibble!
Now thou's turn'd out, for a' thy trouble,
But house or hald,
To thole the winter's sleety dribble
An' cranreuch cauld!

But, Mousie, thou art no thy lane
In proving foresight may be vain:
The best laid schemes o' mice an' men
Gang aft a-gley,
An' lea'e us nought but grief an'pain,
For promised joy.

Still thou art blest, compared wi' me!
The present only toucheth thee:
But, och! I backward cast my e'e
On prospects drear!
An' forward, tho' I canna see,
I guess and fear!

R. BURNS

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by

C.R.B. WATSON

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ABSTRACT

Small mammal and vegetation communities in the Marula/Knobthorn savanna (MKN) and *Acacia welwitschii* woodland (ACW) landscapes of the Kruger National Park were monitored through 13 months of drought and 10 months of post-drought conditions. Small mammal community dynamics, and population dynamics of *Saccostomus campestris*, *Praomys coucha*, and *Praomys natalensis* were examined. Body condition and the influence of vegetation communities and microhabitat availability on community and population regulation were assessed.

During the drought, diversity was high while density was low (<4 a/h) in both habitats. Extrinsic regulation through food and predators is suggested. High density and individual growth occurred in both habitats in the early post-drought. By late post drought, ACW diversity was high but low in MKN. Density and individual growth increased in MKN but not in ACW. Intrinsic regulation by limited breeding season, and extrinsic regulation by food, in each landscape respectively, are suggested. A model of the effects of drought on the food supply in each habitat is proposed.

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ACKNOWLEDGEMENTS

My interest in the biological sciences stems from a life long amazement at the efficient yet intricate workings of the animal body. The body is like that of a puzzle, a whole with many pieces, each with its own function and place, each piece as important as the other in completing the whole. Despite the orderliness of the body and unlike the puzzle, flexibility is not entirely lost and the struggle to maintain optimum functioning is perpetual. Although my interest in natural history was always present, my BSc degree in animal sciences and pre-veterinary medicine (University of New Hampshire, USA) and later experience in muscular dystrophy research (London, UK) kept my focus on the individual. It wasn't until I started assisting my husband in his doctoral study on the Bateleur Eagle (Terathopius ecaudatus) in the Kruger National Park that I began to see, with equal wonder, the functioning of a community as many parts to an amazingly efficient whole. For the opportunity provided by this Masters study to explore this fascinating area of ecological study I will always be thankful.

I would like to acknowledge the support of three institutions and the individuals associated with them for their widespread assistance during this study. First, the support given by the National Parks Board, in particular, Dr. Salmon Joubert, now the chief warden of the Kruger National Park, who first suggested working on small mammals and arranged for the study to proceed. Many other Parks Board employees also contributed to this study either in terms of physical labour or moral support and to these people, Andre Potgieter, Willem Gertenbach, Leo Braack, Don English, and Wayne Vos from Skukuza and Corbus Botha the local ranger, Peter and Daleen Palm and Robbie and Sandy Lombard at Satara I want to express my sincere thanks.

Secondly, the support of the University of Pretoria, especially the Mammal Research Institute and in particular, Prof. John Skinner who was willing to accept me, an unknown academic entity, as a Masters candidate, took over as co-supervisor when the need arose and whose help with the written thesis is

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gratefully acknowledged. My appreciation and thanks also go to Prof. Jan Nel who's enthusiastic support and help in the initial stages of the study were readily given. Various faculty members have also substantially assisted me and I'd like to thank Dr. Neil Fairall for help with the tritiated water technique and the writing of Chapter 7, Dr. Hector Dott for his ever helpful and constructive criticisms of preliminary drafts of this thesis and Dr. Marthan Bester for his translation of the summary into the opsomming. In addition, various fellow students also helped enormously with discussions, ideas and labour and I sincerely thank Joe and Inge Henschel, Albert Van Jaarsveld, Rob Davies, Daan Buys, Andrew McKenzie and Mike Gibson. The assistance of the National Herbarium and the University of Pretoria's herbarium, especially Mrs. Ensie Du Plessis in identifying the grass specimens is gratefully acknowledged as well as the assistance of Mr. Spreeth in the Dept. of Agriculture for his help in the fat extraction procedures.

Thirdly, I gratefully acknowledge the financial assistance provided by the CSIR during four years of this study.

Many individuals, friends and family have also contributed to the successful completion of this work. Prof. Winston Trollope, University of Fort Hare, for his help with the pasture disc meter, Dr. Doug Gordon, Transvaal Museum, for all his encouragement and willingness to electrophoretically analyse all the Praomys blood samples and to Dr. Mike Watkeys for his friendship and help in arranging for the chemical analysis of the soil samples. I would also like to express my heartfelt thanks to my family back in the USA, particularly my parents for their unfailing faith in my abilities and their continued efforts to help me in what ever way they could despite the difficulties of the distance separating us. Equally supportive was my husband's family and to my mother-in-law, Helen, special thanks for always having an open house and a warm heart waiting for us on our returns to Jo'burg and to the rest of the family for all their interest and understanding. I would like to give special thanks also to friends past and present at Gobabeb, our present home in the Namib Desert, for their support, encouragement and cheerful understanding which I have greatly valued during the less

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enjoyable stages of writing up. In particular to Dr. Mary Seely for giving me space and time to finish the work on small mammals before I started with detritus, and also to Debaran Kelso, Carole Roberts, Susan Gut, Janet Rasmussen, Bob Pietruszka and Dave and Helen Boyer.

Finally, I would like to dedicate this thesis to two very special friends. To Big Dad, the pouched mouse (Saccostomus campestris), who befriended us in the Kruger and was with us in the desert until his death last year. His friendly, cheerful and busy little countenance was an endless source of inspiration and amusement. Sundowners will never quite be the same without him on my shoulder. Secondly, I dedicate this work to my husband, Rick, without whose love and support this could never have been finished. Despite the demands of his own doctoral research, he gave me his time to walk traplines in all sorts of weather and endured numerous hardships from mouse-inflicted wounds to being swept down flooded streams while trying to rescue my traps. The extent of my appreciation for his patience and support especially during the final stages can never be expressed.

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COLLECTED REPRINTS

Published or submitted articles already emanating from this study.

1. Watson, C.R.B. & Watson, R.T. 1985
2. Gordon, D.H. & Watson, C.R.B. 1986
3. Watson, C.R.B. & Watson, R.T. 1986
4. Watson, C.R.B. Percentage cover manuscript for submission to J. Range Manage.

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CHAPTER ONE

INTRODUCTION

Small mammals have received the attention of man for thousands of years which many references in the Old Testament bear witness to (Elton 1942). The early scientific accounts of small mammals reflected their notoriety as agricultural pests and carriers of such diseases as bubonic plague, rabies and typhus (Davis 1942, 1948, 1953, Bouliere 1975, Myllymaki 1975, De Graaff 1981). While the pathological and agricultural importance of small mammals has not diminished, especially in less-developed countries (Davis 1966), their importance to science today has broadened and they have become subjects for medical (Davis 1963, Gordon & Rautenbach 1980), ecological (Lidicker 1966, Watts 1969, Hafner 1977), behavioural (Spencer & Cameron 1983, Ostfeld 1985) and physiological research (Pearson 1960, McNab 1963, Holleman & Dieterich 1973, Kenagy 1973).

Small mammals, here defined as free-living small rodents or shrews (<120 g) following the stricter useage of Delany (1976), have many characteristics which make them invaluable for mammalian ecological studies, both at the community and the population levels. These include their small size, short life cycle and high reproductive capacity (Delany 1976). Whereas their high metabolic requirements make small mammals particularly vulnerable to environmental deterioration, their high fecundity enables them to repopulate areas quickly when conditions improve. Small mammals are known to cope efficiently with and recover quickly from ecological disasters which would cause local extinction of larger terrestrial mammals (Bouliere 1975). Furthermore, the short life span allows relatively easy study of several generations which aids genetic (Krebs 1971, Smith, Teska & Smith 1984) as well as ecological and behavioural studies. These characteristics plus the relative ease with which small mammal communities and their local habitats can be manipulated have made them increasingly important to ecologists for experimental examination of various current theories in population and community ecology (Rosenzweig 1973, Schroder & Rosenzweig 1975, Price 1978, Whitford, Dick-Peddie, Walters & Ludwig 1978, Geier & Best 1980, Parmenter & MacMahon 1983, Spencer & Cameron 1985, Bowers 1986). In a similar fashion, these characteristics make small mammal communities excellent indicators of habitat condition and their use in environmental monitoring programmes is also increasing (Beatley 1976, Ghiselin 1980, Racey & Euler 1982, Steele, Bayn & Grant 1984).

Population regulation in small mammals is probably best exemplified by the tremendous fluctuations in numbers of the voles and lemmings of the northern hemisphere (Krebs & Myers 1974). Although hypotheses concerning how and why population regulation occurs are many, most can be divided into four distinct but related concepts. First is density-dependent regulation which is said to occur when the influence of various factors on individuals in a population or community varies as the number of individuals per unit area changes (Ricklefs 1973). Food, shelter, breeding sites as well as numbers of predators may work as density-dependent factors. However, when and how these factors start to influence the small mammals depends on the limits of each species's ecological flexibility. Second is density-independent regulation which can occur when external factors such as weather, fire, and water, influence individuals in a population or community regardless of the number of individuals per unit area (Ricklefs 1973).

Related to the first two concepts but expressed from a slightly different angle is the third idea of intrinsic or self-regulation, where population regulation occurs as a result of things animals do rather than by direct interaction with resources or predation (Caughley & Krebs 1983). Examples of this type of regulation would be limited breeding seasons, spacing behaviour and/or dispersal (Grant 1970, Grant & Morris 1971, Krebs 1979, Spencer & Cameron 1983). The fourth concept is population regulation by extrinsic means, that is regulation which results from factors outside of the animals' inherent behaviours. This would pertain to such factors as resource availability, predators, disease, or weather (Caughley & Krebs

1983). Extrinsic factors, then, could encompass both density-dependent and density-independent factors while behaviours denoting intrinsic regulation may be triggered by various extrinsic circumstances. Population regulation and especially community regulation is rarely one alternative or the other but the result of the interactions between the different mechanisms (Caughley & Krebs 1983).

How population regulation in small mammal communities in Africa fit in with these concepts and which factors are important in their regulation are questions which have not yet been addressed in small mammal studies on the African continent. The majority of the larger studies, especially the early ones, tend to be expanded species checklists with an emphasis on taxonomy (Sanderson 1940, Roberts 1951), while later works include some reference to their general biology and habitat distribution (Ansell 1960, Gorman & Robertson 1981, Rautenbach 1982). More specific studies on Africa's small mammals have expanded rapidly in recent years to include works on reproduction (Delany 1964, Sheppe 1973, Neal 1982a, 1982b, 1984a, Perrin 1984), behaviour (Choate 1972, Cheeseman 1977, Earl 1980, Packer 1980), diet and digestion (Field 1975, Perrin & Maddock 1983, Churchfield 1985, Perrin & Kokkin 1986), age determination (Perrin 1979, Henschel, David & Jarvis 1982, Taylor, Jarvis, Crowe & Davies 1985), physiology (Withers, Louw & Henschel 1980, Haim 1981, Perrin 1981) and habitat associations (Neal 1970, Sheppe 1973, Bond, Ferguson & Forsyth 1980, Rowe-Rowe & Lowry 1982). While a few studies have dealt with population dynamics in general (Cheeseman & Delany 1977, Chidumayo 1980), I was unable to find any published studies which specifically addressed population regulation and the factors which may be involved.

The relatively undisturbed ecosystem of the Kruger National Park represents an ideal situation in which to study natural population regulation of a small mammal community because the small mammal and predator communities as well as the habitats have been largely unaffected by man, except for the triennial burning regime, since the 1920's (Braack 1983). Small mammals are an important component of the system of energy flow through any ecosystem as they are both consumers and prey (Golley,

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Ryszkowski & Sokur 1975). However, in the Kruger National Park only Kern's (1981) study has investigated the small mammals to any significant degree. He showed that the triennial rotation burning regime, employed for the control of bush encroachment and fire risk (Brynard 1964), maintained diversity in the small mammal communities by substantially altering the habitat structure. How small mammal communities are regulated in the interim between fires and exactly what their important ecological functions are in the park are questions so far unanswered.

The focus of the present study, which was conducted from November1982 to September 1984, was to examine the influences of habitat structure on small mammal communities, their composition and dynamics. Two distinct habitats, the _Sclerocarya_ _caffra/ Acacia_ _nigrescens_ savanna, commonly known as the Marula/ Knobthorn savanna, and the _Acacia_ _welwitschii_ woodland thicket landscapes (Gertenbach 1983), were chosen for a comparative study of small mammal and vegetation communities. These habitats were chosen for a number of reasons. First, the two habitats were adjacent (see Fig. 6) with no physical barrier between them thus the small mammal communities were free to establish themselves as each habitat allowed. Secondly, the geographic proximity of the two habitats meant that each vegetation community would experience the same local climatic occurrences. Thirdly, while the vegetation communities were generally similar in composition, they were distinctly different in habitat structure. And finally, each landscape had areas (blocks) which were on the same rotational burning schedule and which were last burned in August 1981.

Kern's (1981) study tended to emphasise the effect of fire on small mammals through the first post-burn year and he showed that prior to burning, diversity was low but populations were high. After burning, the resident populations soon crashed, however, as soon as the vegetation began to recover, diversity increased with the arrival of pioneer species. Higher densities, however, did not return until cover was once again reasonable, by the middle to end of the rainy season. The present study was initially designed to follow small mammal communities through the second and third years after the burn when the vegetation had

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fully recovered and was reaching its allowed three year climax community. However, the severe drought which occurred over southern Africa in late 1981 to late 1983 (Tyson 1986) did not allow vegetation to recover until it rained sufficiently again in the 1983/84 summer season. This resulted in monitoring small mammals through approximately one summer of extreme drought and one summer of normal rainfall. These climatic extremes added a further dimension to the main objectives of the study which were

1. to establish appropriate field techniques for monitoring small mammals monitoring in the Kruger National Park.
2. to compare small mammal communities in two habitats over an approximate two year period by determining community composition and monitoring community responses to natural changes in habitat conditions.
3. to determine which factor/s may have been influential in regulating the small mammal communities in each habitat and in both climatic periods.

In order to present the results of this two year study, the thesis is structured in the following manner: after an account of the general study areas and the historic and recent climatic conditions (Chapter 2), the vegetation communities in the two habitats are examined in terms of their composition, structure and dynamics (Chapter 3). Then the structure and dynamics of the small mammal communities as a whole are presented in Chapter 4. This is followed by an investigation into the role of intrinsic regulation by analysing the population dynamics of the three dominant species, _Saccostomus campestris_, _Praomys coucha_, and _Praomys natalensis_, (Chapter 5) while Chapter 6 considers the extrinsic factor of microhabitat preferences and especially the availability of cover in each habitat for the same three species. Chapter 7 then considers the influence of food by comparing diet composition and body condition. In the final discussion (Chapter 8), the interactions between small mammal communities, species themselves, and habitats are discussed in the light of community and population regulation. This is aided by the presentation of a model of the vegetation dynamics in each habitat over the two

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climatic periods. In addition, ideas for future investigations to help clarify the role of small mammals in the Kruger National Park are suggested. Various appendices are also attached containing supplementary information which is referred to in the text and might be of interest to the reader. These include, chemical analyses of the soils, vegetation community composition in the four trapping sites, the raw data on microhabitat availability and the distribution of species captures, and morphological measurements of the snap-trapped animals. Finally, recommendations for trapping techniques to use in further studies of some of the basic aspects of small mammal ecology in the Kruger National Park are offered. These are presented in the form of a series of flow diagrams which outline various potential study objectives and the possible methods and references necessary for achieving the stated aims.

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CHAPTER TWO

STUDY AREA

INTRODUCTION

In this chapter, I give the background information on the study area necessary for the geographical and environmental orientation of the reader. First, a brief introduction to the Kruger National Park is given by discussing its location, zoogeographical classification and its general climatic, geographical and topographical patterns. Secondly, important aspects of the topography, geology, soils, rainfall and temperatures of the Satara region and particularly the two landscapes chosen for the study are highlighted. Finally, brief descriptions of the two landscapes chosen for the study and the reasons for their choice, including the importance of the triennial rotation burning scheme, are outlined. The exact study site locations are given and their local physiognomy and unique physical structures are described in relation to trap line orientation.

KRUGER NATIONAL PARK

The Kruger National Park (KNP) occupies 1 948 528 ha in the northeast corner of the Transvaal Province of the Republic of South Africa (Fig. 1). It lies between 22°20' to 25°31' latitude south and 30°50' to 32°02' longitude east (Pienaar, Rautenbach & De Graaf 1980). Roughly 350 km long and 90 km wide, the KNP coincides with three international borders, that of Zimbabwe to the north, Mocambique to the east and the Republic of Venda in the northwest. The western border has a discontinuous regional boundary with the black homeland of Gazankulu and the Transvaal province (Fig. 2a). In ecological terms, the KNP has three natural borders. The Levuvhu and Limpopo rivers which delineate the northern border, the Lebombo mountains which lie along the eastern border and the Crocodile river which forms the southern border (Braack 1983). The western border is an arbitrary line which merely divides the KNP from private lands. Much of the

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land to the immediate west is used for game farming or as private nature reserves which tends to act as an ecological buffer separating the KNP from areas of agricultural land use further west.

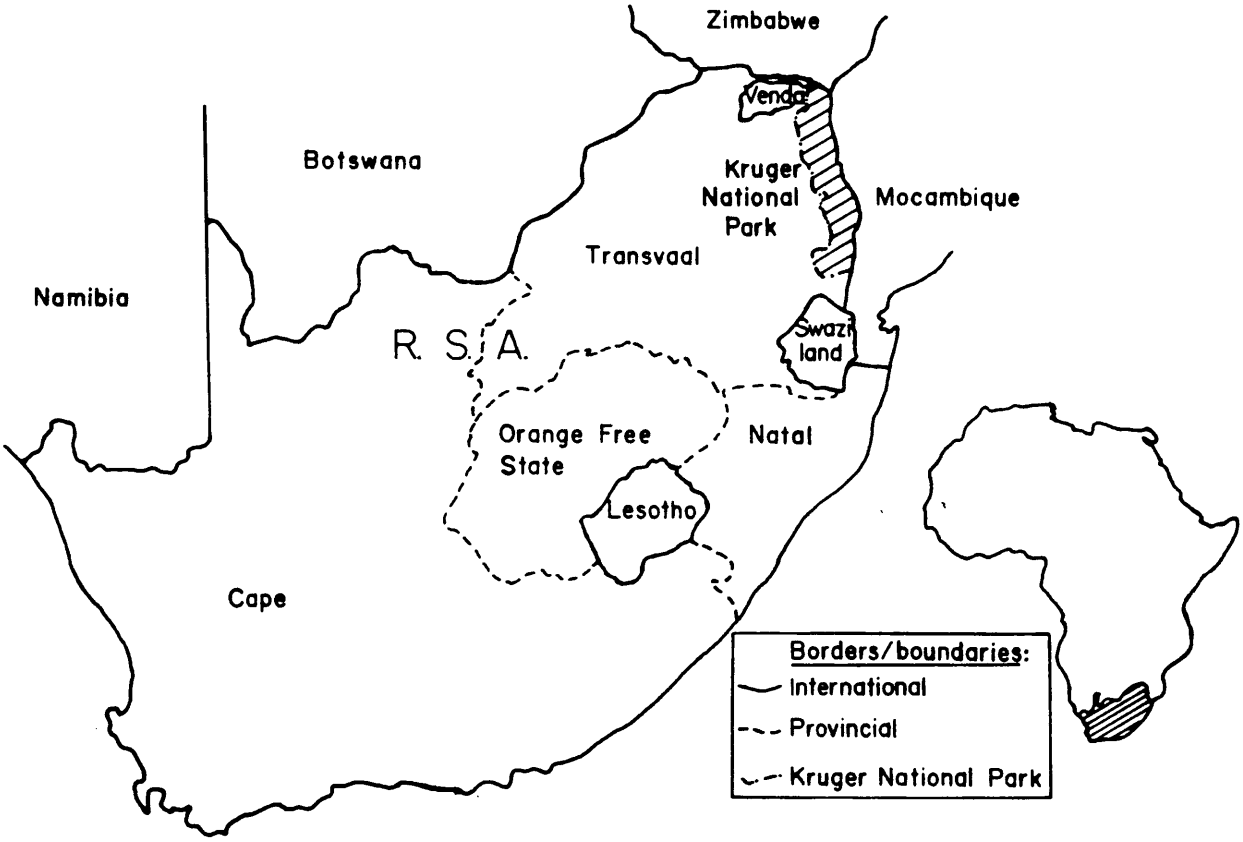

Figure 1: Map of southern Africa showing international and provincial borders and the Kruger National Park (shaded). Inset: The African continent with the Republic of South Africa shaded.

Zoogeographically, the KNP lies within both the Southern Savanna biotic zone of Moreau (Davis 1962) and the tropical arid savanna region outlined by Huntley (1982). Rautenbach (1978) has further classified the region as the Eastern Transvaal Lowveld biotic zone. Though broadly classified into a single biotic zone, the KNP has many distinct ecological regions within it (Pienaar *et al.* 1980) and variations in rainfall, topography, geology and associated vegetation communities are apparent throughout the park (Fig. 2).

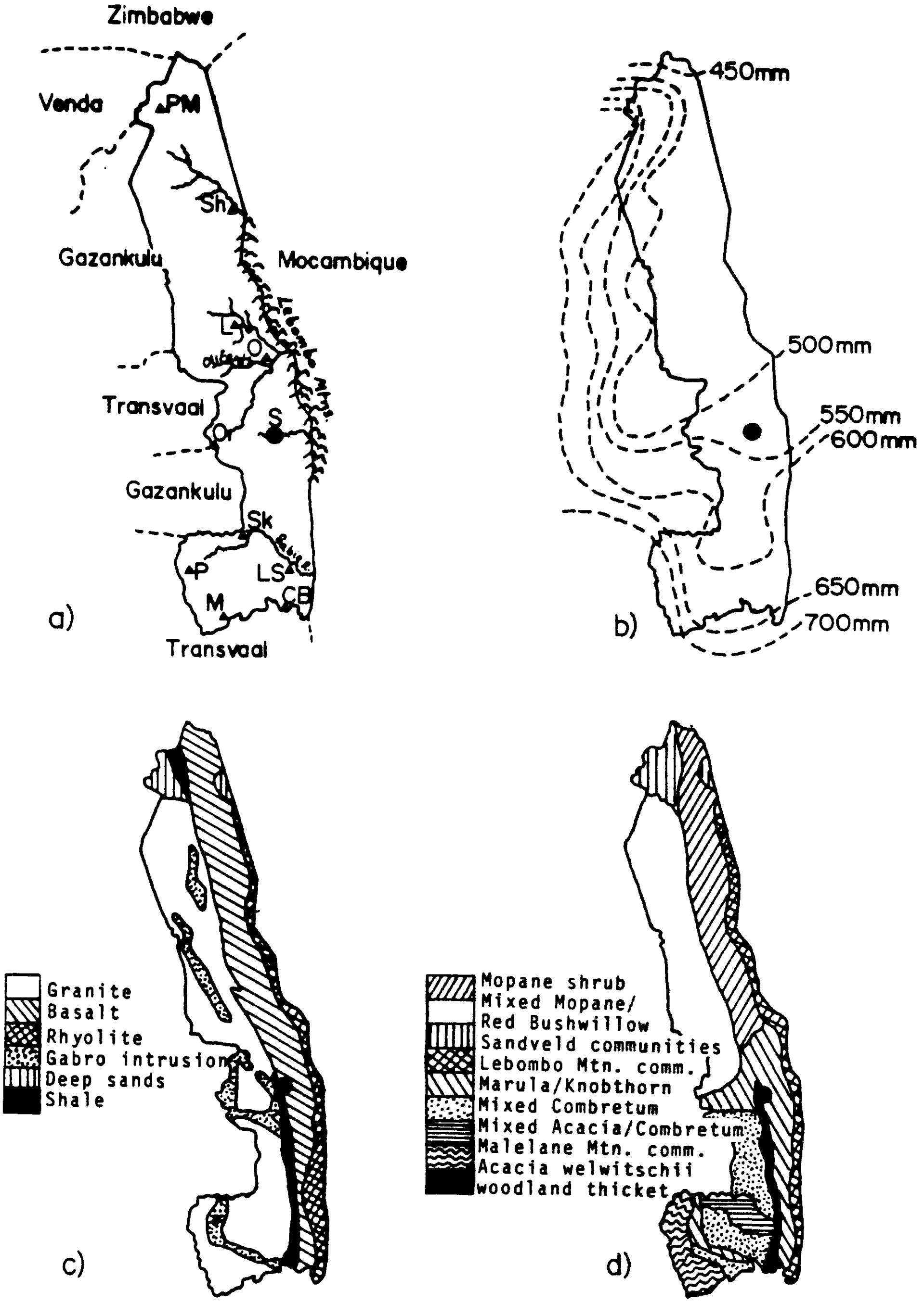

Figure 2: The Kruger National Park. ● Satara restcamp.
a) Political and geographical features, ▲ other restcamps namely, PM-Punda Maria, Sh-Shingwedzi, L-Letaba, O-Olifants, S-Satara, Or-Orpen, Sk-Skukuza, P-Pretoriuskop, LS-Lower Sabie, M-Malelane, CB-Crocodile Bridge. b) Annual average rainfall patterns, 450-700 mm isohytes. c) Simplified geological map. d) Simplified vegetation map. Maps obtained from Kruger National Park Research Division.

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The KNP lies in the summer rainfall region of southern Africa. The rainy season extends from October to April with rainfall peaking between December and February. Mean annual precipitation varies along a north/south gradient with 400-500mm /annum in the north and 600-700 mm/annum in the south (Fig. 2b). Analysis of the annual rainfall data from the last 60 years suggests an 8 to 12 year cycle of wet and dry periods (Gertenbach 1980, Tyson 1986) which placed this study at the start of a new 10 year dry cycle.

The topography of the interior of the park is generally flat with scattered small hills. Throughout the southern region and along the eastern and northern perimeters mountains and large hills predominate.

The major geological substrates are rhyolites in the far east, basalts in the central east and granites in the west. The transition from basalt to granite has created a unique strip of Ecca shales which runs longitudinally through the center of the southern region of the park (Fig. 2c and 4).

Due to different combinations of the rainfall, topography and geology, the vegetation is quite diverse. Gertenbach (1983) divided the vegetation into 35 distinct landscape types for the purpose of practical conservation management. He defines a landscape as "an area with a specific geomorphology, macroclimate, soil and vegetation pattern and associated fauna". A simplified vegetation map of the KNP is shown in Fig. 2d.

SATARA REGION

This study was conducted in two landscapes in the Satara region of the KNP. Satara, lying beside the Shitsikana spruit, is centrally located approximately 90km from the Olifants (to north) and Sabie (to south) rivers and lies in the eastern half of the park ($24^{o}24$'S, $31^{o}47$'E) (Fig. 2a). The Nwanedzi river and the Sweni spruit (3 km and 10 km south respectively) are its closest naturally perennial waters (Fig. 3). However, at Satara the Shitsikana spruit, which should be a dry stream bed, flows for approximately 1 km because of a high water table resulting from the frequent waterings of camp lawns and leaks from the camp's main water pipe. The vegetation in the immediate surroundings of the Shitsikana is lush and did not degenerate as greatly during the drought as the natural veld.

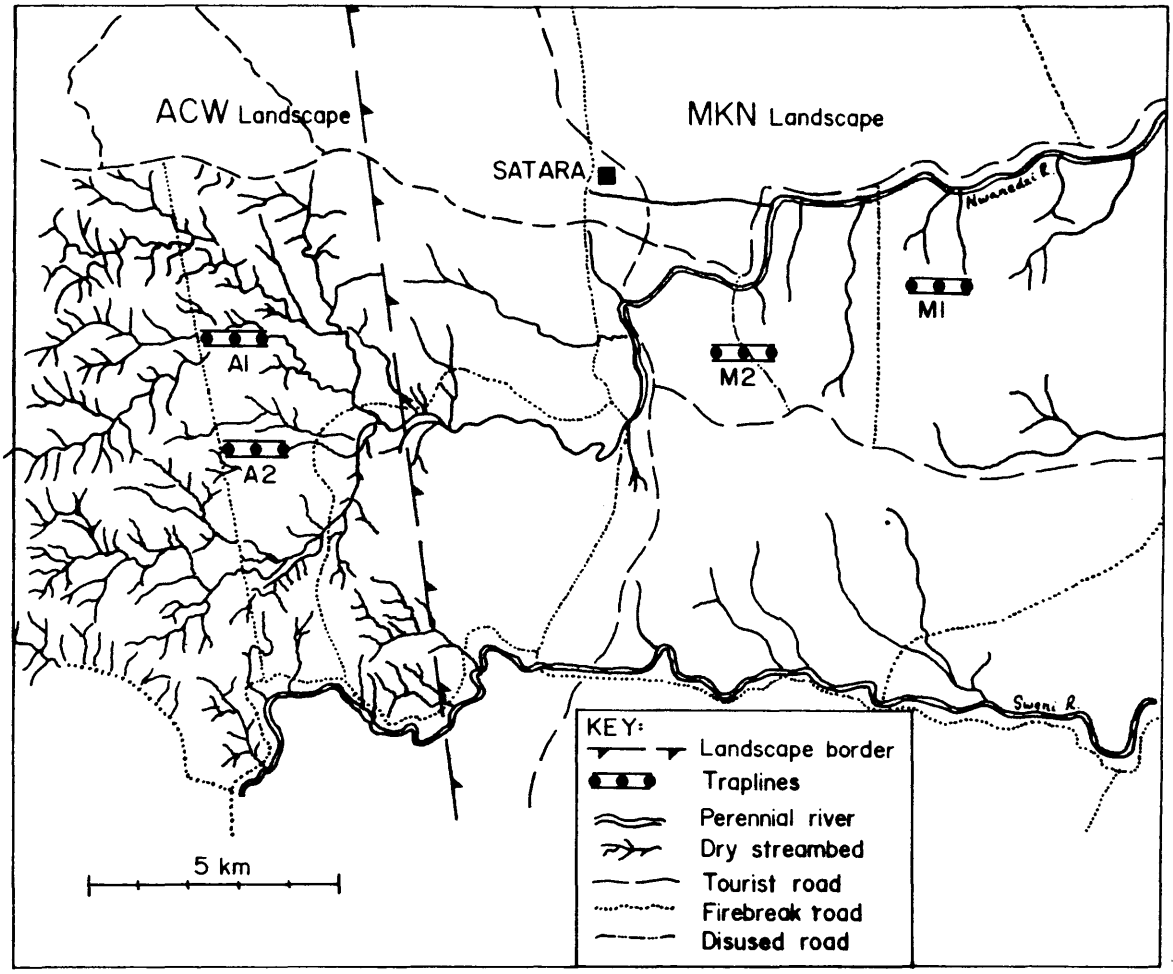

Figure 3: Map of Satara region of the KNP showing the orientation of the traplines within each landscape. Firebreak roads delineate the boundaries of different burning blocks.

Topography, geology and soils

The geology and related topography of the Satara region are shown in Fig. 4 (adapted from Webber 1979). Rolling hills occur in the west which gradually flatten out into low lying plains in the central and eastern regions. The elevation then rises sharply into the Lebombo mountains in the far east. Granite underlies the western hills while Ecca sandstone and shales emerge where the granite meets the basalt of the eastern plains. Rhyolite underlies the Lebombo mountains.

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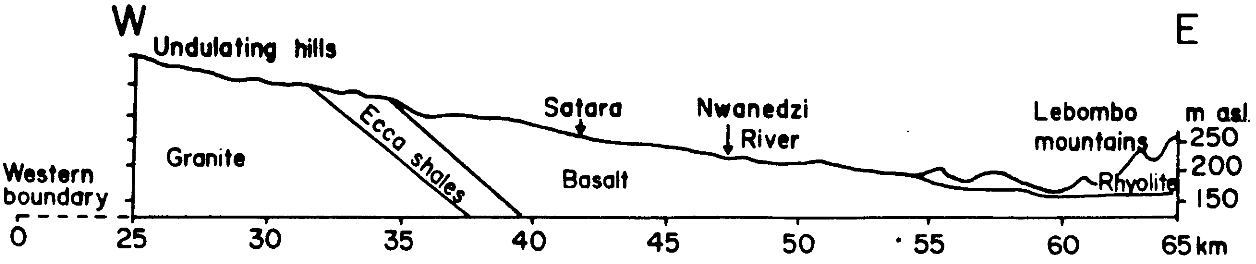

Figure 4: The relationship between topography and geology in the Satara region of the KNP. (Adapted from Fig. 2.5, Webber 1979).

The two landscapes chosen for the present study occur on the eastern basalt plains and on the thin belt of Ecca shales (Fig. 4). The remainder of the study area descriptions will deal only with these two areas.

The soil types which occur in these landscapes correspond strongly with their geological bases. The basaltic plains form a heavy black or dark red clay soil (Webber 1979). The clay content varies from 25 to 50% and it is rich in plant nutrients (Gertenbach 1983). The Ecca shales form a duplex soil of fine and medium grained sands overlying a clay substrate (Webber 1979). This type of soil is highly susceptible to erosion and weathering and tends to be nutrient poor (Webber 1979, Gertenbach 1983). Chemical analyses of the soil composition is given in Appenidix I.

Rainfall and temperature

Satara lies between the 500 and 550 mm average annual rainfall isohyet (Fig. 2b) (Gertenbach 1980). The total tri-monthly rainfall figures for the last five years and the tri-monthly rainfall pattern, averaged over the last 50 years (KNP research division, unpublished data) are presented in Fig. 5. The 1980/81 summer precipitation was 151% above average. Severe drought was experienced during the following two summers. Precipitation in the 1981/82 and 1982/83 seasons was well below average (76 and 66% respectively). The increased precipitation in the September/ October/ November period of the 1981/82 season was the result of one major storm in November when greater than 100 mm of rain fell over a three to four day period. A similar

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situation occurred 16 months later in the March/April/May period of the 1982/83 rainy season when over 100 mm fell in one 24 h period at the end of March. In these storms a lot of rain fell but without substantial follow-up rains, they did little to alleviate the drought and in the long term, probably compounded the drought situation by creating a small flush of green vegetation which was promptly overgrazed by the larger herbivores in the subsequent hot dry conditions.

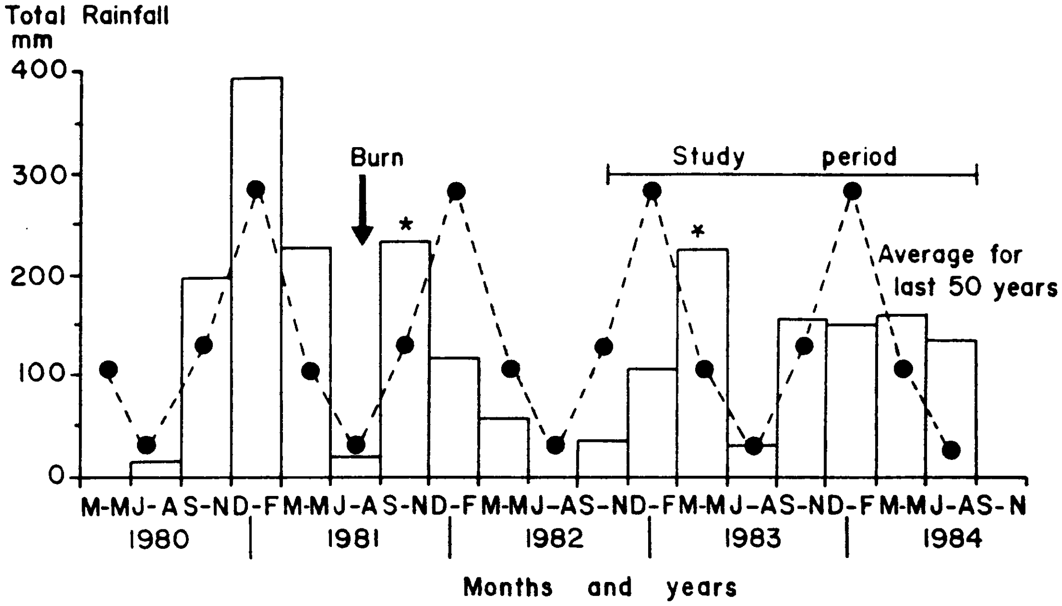

Figure 5: Tri-monthly rainfall records from Satara restcamp, KNP (bar graph), for the period March 1980 to August 1984. The 50 year tri-monthly mean rainfall (dotted line) is included for comparison. *- single storm producing over 100 mm. (unpublished rainfall records from the KNP Research Division).

The mean maximum daily temperature for the Satara region in summer is 33^{o}C while the mean minimum is 19^{o}C. The winter mean maximum temperature is 27^{o}C and the mean minimum is 8^{o}C (Gertenbach 1983). The mean temperatures I recorded, while trapping, agree with Gertenbach's records but also show that the range of temperature fluctuations in any one season was quite high (Table 1).

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Table 1: The maximum and minimum mean temperatures (^{o}C) and the seasonal range records for the Satara region of the Kruger National Park for the years 1982 to 1984. * - data not recorded.

		November/December		March/April		July/August	
		$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range
82/83	Max.	*	*	32.4	21-41	28.3	20-36
	Min.	*	*	19.9	16-26	12.2	6-18
83/84	Max.	34.2	23-44	28.7	22-38	26.8	14-34
	Min.	19.9	14-25	18.4	12-23	12.1	6-17

Burning regime

The park has an overall policy of triennial rotational burning during the August to October period. This policy is to facilitate control of bush encroachment and to reduce the risks of large veld fires. The entire park is divided into blocks of various sizes by the maintenance of annually graded firebreak roads. One third of these blocks are burnt each year which results in each block being burned once in the three year cycle. Blocks adjoining the restcamps, however, are burnt annually to maximally reduce the risk of veld fire. The exact time of burn is dependent on the start of the rainy season in that particular year (Brynard 1964). In general, burning within each ranger's area commences after the first rainfall of 50 mm or more. The burning blocks and firebreak roads in the Satara area are shown in Fig. 3. The four small mammal study sites were situated in three different burning blocks but with identical burning schedules. These blocks and thus all four study sites were burned in August 1981.

As only 18-24 months were available for fieldwork, trapping was to start one year after burn. This allowed the vegetation and small mammal communities a recovery and reestablishment period (Kern 1981). This meant that trapping would continue through to the vegetation's allowed climax, that is until the blocks were due to be burned again in October 1984. The 1981

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burns were performed on schedule, the two year drought which followed, however, curtailed the expected vegetation recovery process until the start of the 1983/84 rainy season which, although still lower than average (91%), had a more consistent rainfall pattern (see Chapter 3).

Landscape classification

Gertenbach (1983) identified 35 landscape types in the KNP. Of these landscape types, two which occur in the immediate Satara area were chosen for the contrasting habitats they would offer small mammals. The two chosen were the *Sclerocarya caffra*/*Acacia nigrescens* savanna (commonly called the Marula/Knobthorn savanna) on clay soil and the *Acacia welwitschii* thickets on a sandy soil (Fig. 2c and 2d). The Marula/Knobthorn savanna (MKN) is on the flat basaltic plains east of Satara and forms one of the largest landscape types in the park. It occupies 1 411 km^2 which is 7,2% of the total area of the KNP (Gertenbach 1983). It is an open woodland savanna with a highly dominant field layer with few annual waterways (Fig. 3 and 6 (right side)). This landscape offers a generally homogenous grassland habitat for a small mammal community and was one of the landscape types investigated by Kern (1981) in his small mammal - fire relations study conducted in 1977/78.

The *Acacia welwitschii* thicket (ACW), west of Satara, occurs on sandy soils in the centrally located Ecca shales. This landscape, though small in area occuping only 2,7% of the KNP, has a unique vegetation community (Gertenbach 1983). It is a heterogenous habitat characterised by a mosaic of woodland, grassland and bare ground areas and is inundated with annual waterways (Fig. 3 and 6 (left side)). These two factors result in the ACW landscape having a distinctly patchy appearance where microhabitats can change quite abruptly. The two landscape types remained distinct even along their common border (Fig. 6). This negated the problem of avoiding transitional vegetation communities when choosing specific study sites. A complete listing of the tree and grass species identified in each trapping site is given in Appendix II.

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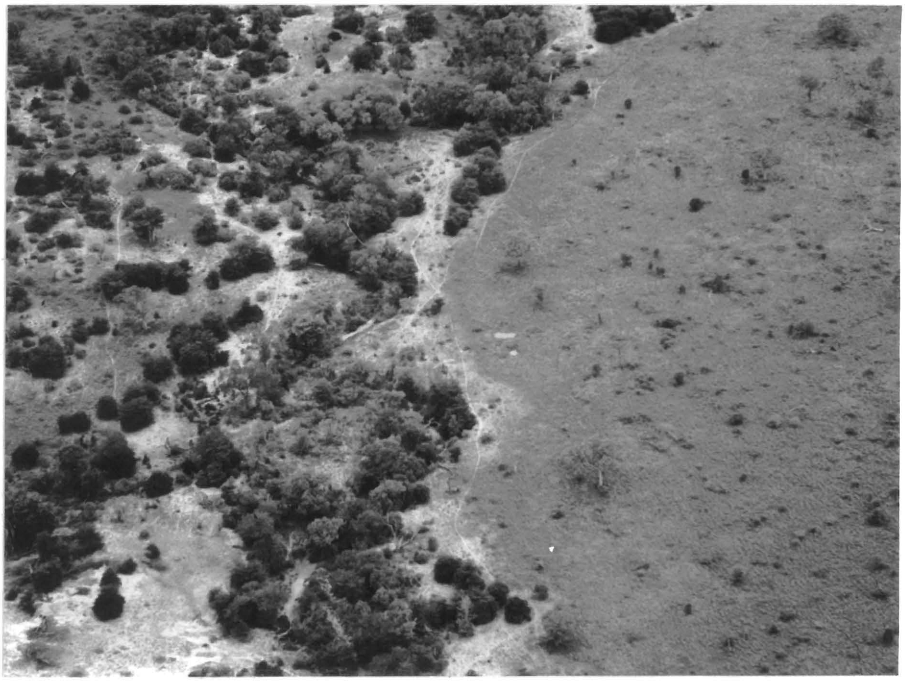

Figure 6: Aerial view of the Marula/Knobthorn savanna (right) and the *Acacia welwitschii* woodland thicket (left) landscapes of the KNP. Note the abrupt transition between the two landscapes.

Trapping sites

Two trapping sites in each landscape were used for the assessment of the small mammal communities. Study site choice in the MKN was virtually unlimited. The vegetation and physiogonomy were very consistent, thus almost any site would have been a good representation of this grassland habitat. The first study site (M1) was approximately 10 km east and 2 km south of Satara (Fig. 3). This study site bisected a small rocky ridge (approximately 50 m wide) which ran in a northwest/southeast direction (Fig. 7a). The second MKN study site (M2) was 5 km east and 4 km south of Satara in a different but adjacent burning block. This site was forced to cross an old disused firebreak road because of the course of the Nwanedzi river and the orientation of the tourist road (I had to remain out of sight of tourists). Although the road had been disused for some time, the vegetation on it was still extremely sparse and consisted of mainly pioneer species which were atypical of the habitat. For this reason, trapping across the road and 8m either side was avoided (Fig. 7b). There was a small periodic mud hole present on this study site.

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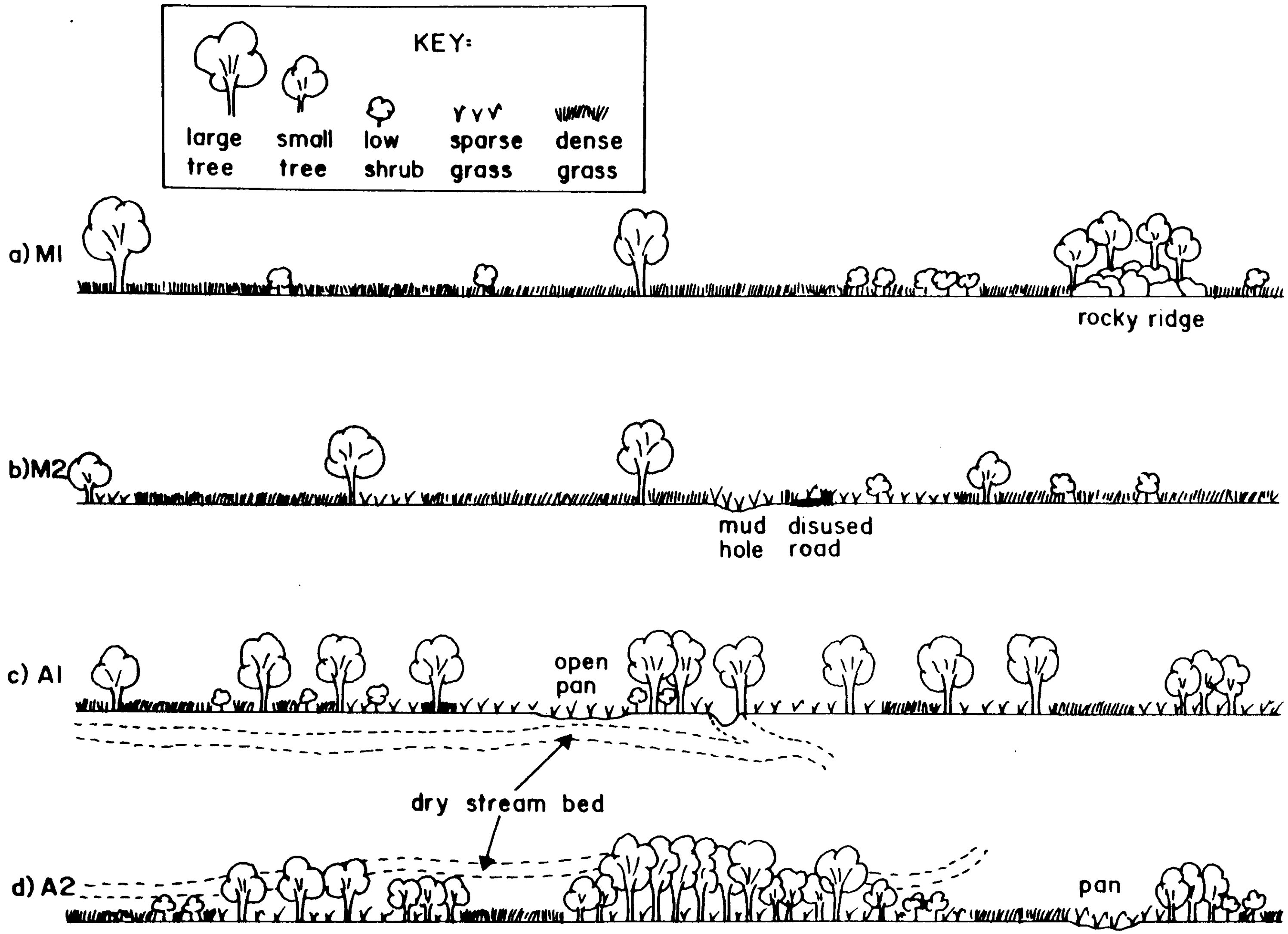

Figure 7: Physiognomic structure and physical features in the four trapping areas in the MKN (M1 and M2) and ACW (A1 and A2) landscapes of the KNP.

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In the ACW, study site choice was limited to the one block which had been burned in 1981. The landscape type as shown in Fig. 2d is very narrow so the size of the block was also a limiting factor. Dry stream beds were a common occurrence (Fig. 3) but as this feature was not commonly available in the MKN habitat and represented a potential threat to trap and small mammal survival if they unexpectedly flooded, attempts were made to avoid them as much as possible. The first ACW study site (A1) was 7 km west and 5 km south of Satara (Fig. 3). To keep other variables constant, however, the trapping line had to cross a small dry streambed (Fig. 7c). The point of crossing though was chosen for its least different vegetation pattern. Trapping in the streambed and along the sides was avoided therefore, a small gap in the regular trap spacing was also present in this study site. The second ACW study site (A2) was 2 km south of A1 (i.e. 7 km west and 7 km south of Satara) (Fig. 3). This trapping site had the greatest variety and distinctness of habitat patches. Areas of pure woodland interspersed with open pans and grasslands were present (Fig. 7d). Details and comparisons of the vegetation communities and their dynamics throughout the two year study period are given in Chapter 3.

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CHAPTER THREE

VEGETATION COMMUNITY STRUCTURE AND DYNAMICS.

INTRODUCTION

Food, water and cover, which may be important for concealment from predators, amelioration of the physical environment or as a trap for food material, are the essential resources a macrohabitat must provide for the successful and sustained existence of an animal community (Gysel & Lyon 1980). It is particularly important that these resources are available within a relatively limited area for terrestrial small mammals because of their small size, relative lack of mobility (as compared to large or flying mammals) and their high metabolic needs. Various macrohabitat components both biological and physical provide these resources. The biological components, primarily the vegetation community, are the most important because as the primary producers, they ultimately provide all these resources and thus strongly define small mammal living conditions. Naturally, to understand the small mammal community, the status of these macrohabitat components must be determined. What resources are available, where, when and how they become available are important questions which need to be answered.

Different combinations of these various components create an assortment of small-scale variations in the macrohabitat which are known as microhabitats. Within these microhabitats, the answers to the above questions may vary quite markedly. The number of species and their abundances have been shown to correlate with diversity and size of the microhabitats available, through each species' ability to differentially utilise the available resources (Rosenzweig 1973, Schoener 1974, Reichman & Oberstein 1977, Price 1978). Thus the capacity of a macrohabitat to sustain a certain number of small mammal species is a result of the diversity within its functional components. Because these resources emanate from biological entities, their availability can be highly variable. Vegetation characteristics, such as growth and senescence of the vegetative parts and the production of seeds, change according to seasonal and aseasonal events. A microhabitat's suitability as a resource provider can change drastically through time.

In the present study, I quantified various components of the vegetation communities to expose the macrohabitat and microhabitat possibilities. These were tree and grass species composition, forb density and distribution, the densities of trees in different height classes, standing grass biomass and percentage grass cover. Physical components are also important in defining a macrohabitat. Three of the trapping sites had unique physical features which influenced the small mammal communities. These were: the rocky ridge which passed through the M1 area, the old disused firebreak road in M2 and the dry water course in A1 (see Figure 7). Each of these features explained to some extent a peculiarity in the small mammal community, however, as these features were not general occurrences, they will be mentioned only as they become relevant in the following chapters.

In this chapter, I quantify the vegetation community characteristics in each trapping site and then compare the results at both the intra- and inter-landscape levels. I show that the conditions present in the intra-landscape trapping sites are sufficiently consistent to define each landscape into a habitat type and to allow generalisations about the habitat differences to be made. Also, vegetation trends over the drought (Sessions 1 - 4) and post-drought (Sessions 5 & 6) periods are compared. Finally, in the Discussion section, I consider how each component and the climatic conditions effected each habitat and thus may ultimately effect the small mammal communities.

METHODS AND MATERIALS

Vegetation Survey

Two trapping sites within each landscape were chosen as representative areas for the study and these were designated M1, M2, A1 and A2 (see Chapter 2). Two parallel traplines, 50 m apart, with 43 trap stations, 20 m apart, per line were established (see Methods Chapter 4 for further details). All the vegetation data was gathered from within a 20 m x 20 m square centrally located around each trap station. This yielded 2 X 43 contiguous 400 m^2 (20 m X 20 m) plots for each trapping site.

As the intention of this chapter, after a comparison of the intra-landscape results, is to show vegetation community trends at the landscape level and to broadly define the macrohabitat each landscape offers, the data for each of the 86 plots are combined and mean values calculated. This results in an extremely intensive stratified sampling survey of each trapping site which is quite unnecessary for the overview presented here but for the analysis of microhabitat preferences (Chapter 6) detailed knowledge of the area around each trap station was essential. The following methods of data collection were performed within each 400 m^2 plot in the four trapping sites.

Trees

Each individual tree was identified to species level and its height (m) estimated. Shrubs which normally grew in a multi-stemmed unit (e.g. *Grewia bicolor*; *Acacia exuvialis*) were recorded as one individual. For species such as *Dichrostachys cinerea* which often existed as single stemmed trees but sometimes developed into dense scrub thickets, an estimate was made of the number of individual bushes in the thicket.

Forbs

Forbs were a definite component of the four vegetation communities but were very difficult to quantify. The lack of an adequate identification aid, their short life histories, sporadic occurrences and their greatly differing growth forms were all confounding factors when assessing species present and their relative abundances. Therefore, only a subjective assessment of forb density and spatial distribution was made. This was achieved by using a scale of increasing abundance from 0 to 5, where 0 = no forbs present; 1 = few scattered forbs; 2 = moderate scattered forbs; 3 = abundant scattered forbs; 4 = large areas with forb cover; 5 = almost total forb coverage.

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Grasses

A stratified random sample was used to determine the grass species composition . Two bisecting perpendicular transects were walked diagonally across each plot (Fig. 8). Every three strides, the grass plant closest to the tip of the right foot was identified to genus and if possible to species. This generated 12 identifications per trap station and 1 032 identifications per trapping site. A sample of each grass species encountered was taken and all identifications were done by the University's herbarium and the National Herbarium, Pretoria.

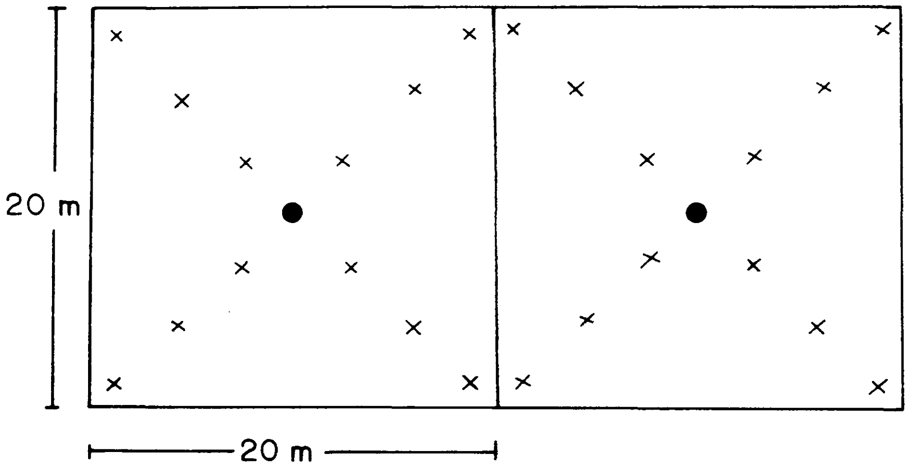

Figure 8: Stratified random sampling pattern used for grass species composition and grass biomass estimates in the 400 m^2 plots surrounding each trap station. ●= trap station, x= point of sampling.

Grass biomass was estimated using the pasture disc meter as suggested by Bransby & Tainton (1977). This method was chosen because of its simplicity, reliability and non-destructive nature (Danckwerts & Trollope 1980, Hardy & Mentis 1985, Trollope & Potgieter 1986). The method is based on a known linear relationship between the disc settling height and the grass dry matter biomass beneath it. The pasture disc meter (see Fig. 1, unpublished manuscript at back of the thesis) measures the disc settling height on the grass beneath it and then a mean disc settling height is used in a pre-determined regression equation

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to yield a standing biomass estimate. To use this method accurately however, a preliminary calibration procedure is required to establish the specific regression equation for the study. Trollope & Potgieter (1986) performed this procedure for the field situations in the Satara area of the KNP. The equation which they generated and which was used in the present study was $y = -3\ 019 + 2\ 260\sqrt{\bar{x}}$, $r^2 = 0{,}90$, where y = dry matter biomass (kg/ha) and $\bar{x}$ = mean disc settling height. Because biomass estimates were calculated for areas of only 400 m^2 (i.e. the plot around each trap station), an estimate in the large-scale units of kg/ha was not particularly relevant. The equation or the biomass estimate was scaled down by a factor of 10 to yield an answer in g/m^2 (e.g. 1 kg/ha = 1000 g/10,000 m^2 = 1,0 g/10 m^2 = 0,1 g/m^2). For the purpose of the present study, all biomass estimates were recorded in g/m^2 but where I discuss the mean values for each trapping site (approximately 3,4 ha) or for the landscapes in general, these will be reported in kg/ha. Twelve measures of disc settling height were taken per trap station (Fig. 8, see unpublished manuscript at back of thesis). A mean grass biomass estimate for each landscape was calculated in each trapping session by combining the biomass estimates obtained from each trapping site.

Grass condition was also noted during each trapping session. The condition of the vegetative parts were noted as brown, green, or changing. The reproductive state was noted as no inflorescence, limited inflorescence, or unlimited inflorescence.

Percentage grass cover was predicted from the biomass estimate by linear regression using the method proposed by Watson (unpublished manuscript, see back of thesis). This method obtains percentage cover from the equation $y = 9{,}01 + 0{,}11x$, $r^2 = 0{,}81$, where y = back-transformed arcsin value * 100 and x = grass biomass estimate (g/m^2). Further details of the method are presented in the included manuscript.

Data and statistical analyses

Trees were classified by height into four categories which could affect the macrohabitat in which a small mammal was living. The height classes were:

1) $\leq$0,5 m - a tree of this height would effectively act as a part of the grass layer. However, it would tend to cause a disruption in the grass layer as the shade of it's foliage could inhibit grass growth.

2) >0,5$\leq$1,0 m - the foliage of a tree this height would extend above the grass layer thereby creating a vertical extension of the grass layer. However, while shading may still inhibit grass growth, the tree itself offers little immediate cover to a small mammal unless dense thickets are formed.

3) >1,0$\leq$4,0 m - This category of tree height probably has the greatest variety of possible effects. A tree in this category can have a larger stem with increased foliage volume thereby creating the possibility of a distinct shading effect. Both stem size and shading may cause some disturbance in the grass layer. Trees of this size also produce a definite middle foliage zone where the grass layer and the tree foliage are visually distinct thereby forming another vegetation zone.

4) >4,0 m - Trees in this category have the largest stems and can have a definite shading effect especially if the trees are clumped, but offer no cover to small mammals. They also produce a distinct upper canopy zone of vegetation and may offer both cover and perches to aerial predators.

Tree structural composition is presented in three forms. First, the mean density of trees per trap station (400 m^2) in each height class. Secondly, as the percentage of the total tree community which occurs in that height class. And thirdly, a density /height class ratio is calculated. This ratio relates the density of trees in each height class to that height class which has the greatest density. This creates a comparative measure which clearly emphasises the degree of dominance within the height classes and shows where the major structural differences are.

The grass structural composition was analysed by categorising each trap station into one of five biomass classes. These classes were 0-100; 101-200; 201-300; 301-400 and >400

g/m^2. Although biomass in itself does not describe a vertical dimension, it is related to the mean disc settling height which is a measure of grass height. The frequency of traps in each biomass class was used to compare the diversity of grass biomass conditions in the four trapping sites during each trapping session.

Shannon's diversity index H' and its associated evenness or relative diversity index J' were calculated whenever a general expression of heterogeneity in the various community aspects was needed. Shannon's diversity index is calculated as

$$H' = (N \log N - \sum n_i \log n_i) / N$$

where N is the total number of individuals in all species or categories and n_i is the number of individuals in the i^{th} species or category. J' is the index of evenness or relative diversity. It is calculated as

$$J' = H' / H\,max'$$

where H' is the diversity index as above and H max' is the maximum possible diversity for the sample N and S, the total number of species or categories (Zar 1984). Maximum possible diversity represents an equal distribution of individuals in all species. Because of this, H max' reduces to log S and therefore is independent of community size. Thus for example, where 100 individuals (N) representing 10 species (S) were found, the maximum possible diversity would be if there were 10 individuals of each species. Evenness (J') is a measure of how close the actual community diversity was to the theoretical maximum possible. The diversity and evenness indices were used for tree and grass species diversity, tree vertical height diversity and grass biomass diversity.

Similarity between the diversity and evenness indices derived in any two trapping sites implies only that there is a similar distribution of individuals in a similar number of species. It makes no statement on the actual identity of those species or their specific abundances. Therefore, Sorensen's coefficient of community similarity (C_N), modified for abundance, was used to compare the similarity of the exact species composition in the four sites. Sorensen's modified coefficient is calculated as

$$C_{Nt} = 2j_{Nt} / (a_{Nt} + b_{Nt})$$

where a_{Nt} is the total number of individuals sampled in habitat a at time t, b_{Nt} is the same in habitat b and j_{Nt} is the sum of the lowest value for the species common to both habitats (Southwood 1978). For example, if three species (a,b,c) were present in both habitats and their numbers were 10, 4 and 6 in habitat x and 3, 8 and 23 in habitat y then j_{Nt} is 13 (3+4+6).

Hutcheson's t-test (Zar 1984) was used to test for significant differences between diversity indices. Mann-Whitney was used to test for significant differences between the mean tree densities in the different height classes and t-tests for equal and unequal variances (as appropriate) were used to test for differences in the grass biomass estimates.

RESULTS

Vegetation Community

Species Composition

Intra- and inter-landscape comparisons of the plant species composition in the four trapping sites showed numerous similarities and differences (Tables 2 and 3, see Appendix II for species lists). First, the number of species present in both the tree and grass communities was very similar within but dissimilar across landscape types. For example, the grass communities in M1 and M2 comprised 12 and 13 species respectively while A1 and A2 communities had 24 and 26 species (Table 2). Secondly, both A1 and A2 had a higher density of trees / ha than either of the MKN areas. Thirdly, besides having similar numbers of species within landscapes, the composition of both tree and grass communities showed greater similarity within landscapes rather than across landscapes (Table 3). Using the grass community as an example again, the M1/M2 and A1/A2 community overlap was 0,82 and 0,74 respectively. The inter-landscape comparisons such as M1/A1 or M2/A2 were all less than 0,61.

Table 2: Tree (A.) and grass (B.) species composition, species diversity (H') and evenness (J') indices in four trapping sites (3,44 ha each) in the MKN and ACW landscapes of the KNP. H' and J' calculated according to Shannon's diversity index. SP75 is the least number of species needed to account for 75% of the community individuals.

	M1	M2	A1	A2
A. Tree Species Composition				
No. of species	32	37	50	49
SP75	4	7	11	15
No. individuals/ ha	429	345	450	486
H'	2,03	2,58	3,09	2,74
J'	0,58	0,71	0,79	0,70
B. Grass Species Composition				
No. of species	12	13	26	24
SP75	2	1	6	4
H'	1,02	0,78	2,31	2,14
J'	0,41	0,30	0,71	0,67

The two MKN sites had lower species diversity and evenness indices than the ACW areas (Table 2). This is supported by the number of species accounting for over 75% of the community's individuals (SP75). In the MKN areas on average 75% of the tree and grass individuals belonged to six tree species and just one grass species. The same parameter in the ACW areas showed that an average of 13 tree and five grass species were needed to account for 75% of each community's individuals. Thus a much higher degree of species dominance occurred in the MKN grass and tree communities than in the ACW. areas.

Table 3: Community similarity values (Sorenson's modified index of community overlap, C_N) between the tree (above the diagonal) and grass (below the diagonal) communities in four trapping sites in the MKN and ACW landscapes of the KNP.

	M1	M2	A1	A2
M1		0,64	0,43	0,27
M2	0,82		0,51	0,40
A1	0,53	0,44		0,59
A2	0,61	0,53	0,74	

Forb distribution and density in the four vegetation communities were strikingly similar (Table 4). In all four trapping sites, the most common occurrence of forbs was in categories 1 and 2 (i.e. a few scattered and a moderate number of scattered forbs). Although M2 had a slightly higher diversity index, caused by the higher frequency of traps with 0 (no forbs) and 5 (almost total forb coverage) ratings, the results do not show large intra- or inter-landscape differences. However, I believe the species composition of the forb communities would have been quite different had the forb species been identified.

Table 4: Frequency of trap stations within the five categories of forb abundance and distribution and Shannon's diversity index (H') comparing the frequency of distribution within the categories for each trapping site in the MKN and ACW landscapes of the KNP. 0 - no forbs present, 1 - few scattered forbs, 2 - moderate scattered forbs, 3 - abundant scattered forbs, 4 - large areas with forb cover, 5 - total forb coverage.

	0	1	2	3	4	5	H'
M1	1	30	32	15	10	1	1,38
M2	9	29	20	18	8	6	1,65
A1	4	28	27	19	12	0	1,46
A2	3	37	27	18	2	3	1,36

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Structural composition

Tables 5 and 6 summarise the structural aspects of the tree and grass communities. Tree height class densities and especially the dominance ratios in M1 and M2 were strikingly similar (Table 5). Both areas had greater than 80% of their trees in the lower two height classes with the greatest density in the ≤0,5 m category. Also, both MKN sites showed a similar decrease in tree density as the height class increased. The density of the various tree heights in A1 and A2 were not as easily interpreted. A1, like the MKN sites had its highest density in the ≤0,5 m height class, but unlike the MKN sites, had its second highest density in the >1,0≤4,0 m category. A2 had its greatest density in the >1,0≤4,0 m with its second highest density in the ≤0,5 m category. While the two dominant height classes in the ACW were the same, the interposition of their importance in A1 and A2 serves to highlight both the similarity of the two trapping sites and the inherent heterogeneity of the ACW landscape itself. Both sites showed a definite bi-level and non-contiguous emphasis in the tree height densities which was quite distinct from the MKN sites with their decreasing gradation in tree density with increasing size.

Table 5: Tree structural composition, diversity (H') and evenness (J') indices in the four trapping sites in the MKN and ACW landscapes of the KNP. D - mean density of trees per trap station in each height class, % - percentage of the total tree community in each height class, Dom. - ratio of numerical dominance in tree height classes.

	M1			M2			A1			A2		
	D	%	Dom.	D	%	Dom.	D	%	Dom.	D	%	Dom.
≤0,5m	7,2	44	1,00	5,9	44	1,00	7,5	43	1,00	5,0	26	0,64
>0,5≤1,0m	6,1	37	0,85	5,2	39	0,88	3,3	19	0,44	4,7	24	0,60
>1,0≤4,0m	3,0	18	0,42	1,9	14	0,32	5,8	33	0,77	7,8	40	1,00
>4,0m	0,2	1	0,03	0,4	3	0,07	0,9	5	0,12	1,9	10	0,24
H'		1,08			1,12			1,20			1,28	
J'		0,78			0,81			0,86			0,93	

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The tree height diversity and evenness indices were also distinctly divided along landscape lines (Table 5). The MKN sites had very similar height diversity, 1,08 and 1,12 and evenness indices of 0,78 and 0,81. Diversity and evenness in the two ACW sites were close but again they both had larger values than the MKN communities.

The grass structural composition changed dramatically as grass heights and consequently grass biomass varied in the two climatic conditions. Because grass structural heterogeneity was not constant throughout the study period, it was assessed during each trapping session (Table 6). Sessions 1, 4 and 6 were chosen to illustrate the grass structural heterogeneity at the start of the study, just before the end of the drought, and in the post-drought conditions respectively. The two ACW sites had consistently wider ranges of disc settling heights and thus grass biomass levels throughout the study. Although the effect of lumping the biomass data into five categories tended to mask the trend somewhat, the biomass diversity and evenness indices indicated a greater heterogeneity in biomass on the ACW sites.

Throughout the vegetation community analyses, consistent patterns in the species and structural composition were shown. Although the intra-landscape comparisons did not yield identical results, the two MKN sites were easily distinguished and distinct from the two ACW sites. comparisons. This allows a fairly safe prediction of what each landscape generally and comparatively offers to the small mammal community. Table 7 summarises the community structure in each landscape. This typified picture is consistent with all the previously mentioned community patterns. The MKN is a comparatively low diversity macrohabitat. It has far fewer species in both the tree and grass communities with lower species diversity and evenness indices than ACW. Vertical diversity is low with the major tree structural input below 1,0m (Table 7). The MKN has most of its vegetation features concentrated around the grass layer while the reduced species richness and low structural heterogeneity combine to create a low diversity and very homogenous macrohabitat.

Table 6: Structural heterogeneity, diversity (H') and evenness (J') of the grass communities in the four trapping sites at the start of the study (Session 1), at the end of the drought (Session 4) and at the end of the study (Session 6) in the MKN and ACW landscapes of the KNP. Structural heterogeneity is based on the number of grass biomass categories present in each site and the range in disc settling height (see text for further details).

	M1	M2	A1	A2
Session 1 (Nov./Dec. 82)				
No. biomass categories	3	4	4	4
Range in disc settling height (cm)	2-6	3-8	1-9	2-9
H'	0,47	0,84	1,17	1,22
J'	0,43	0,61	0,84	0,88
Session 4 (Nov./Dec. 83)				
No. biomass categories	3	4	4	5
Range in disc settling height (cm)	2-5	3-8	1-8	2-11
H'	0,71	1.02	1,07	1,16
J'	0,65	0,74	0,77	0,72
Session 6 (July/Aug. 84)				
No. biomass categories	3	4	5	5
Range in disc settling height (cm)	6-14	4-15	2-24	2-14
H'	0,89	1,06	1,40	1,60
J'	0,81	0,76	0,87	0,99

In contrast, the ACW is a highly diverse and complex macrohabitat. Species and structural heterogeneity are high (Table 7). The emphasis in tree heights is in two distinct zones, $\leq 0,5$ m and $>1,0 \leq 4,0$ m, and the grass biomass conditions varied. These features result in a heterogenous and multilayered macrohabitat.

Table 7: Summary of the generalised tree (A.), grass (B.) and forb (C.) community structure for the MKN and ACW landscapes of the KNP. (*), (**), (***) - significant difference at the P<0,05, 0,01, and 0,001 level respectively, ns - no significant difference.

	MKN	ACW	
A. Tree Community			
No. Species	35	50	
SP75	6	13	
Species H'	2,31	2,91	***
Species J'	0,66	0,75	
Density: n/ha	392	481	
Density: n/trap station	14,9	18,3	***
Density:			
n/height class/trap			
≤0,5m	6,6	6,3	ns
>0,5≤1,0m	5,6	4,0	**
>1,0≤4,0m	2,5	6,8	***
>4,0m	0,3	1,4	***
Structural H'	1,10	1,24	***
Structural J'	0,80	0,90	
B. Grass Community			
No. Species	13	25	
SP75	1	5	
Species H'	0,90	2,22	***
Species J'	0,36	0,69	
Session 1 Structural H'	0,66	1,19	***
Session 4 Structural H'	0,87	1,11	**
Session 6 Structural H'	0,98	1,50	***
C. Forb Community			
Distribution H'	1,51	1,41	ns

Vegetation Dynamics

As various components of the vegetation community changed with prevailing climatic conditions, some aspects of the macrohabitat also changed. These changes were great enough to significantly alter the microhabitat opportunities and the available food suppply.

Tree dynamics

Tree growth and seed production can result in changes in vertical stratification and food supply. Tree growth however, is a long term process and was not considered to have undergone sufficient change to have an effect on the immediate small mammmal community during the present study. Seed production by the trees occurred once during the study after consistent rains started in November 1983. By May/June 1984 virtually all trees had successfully flowered and were producing seeds. The majority of the seed crop, however, especially that of the larger species, was still on the trees by the end of the study in August 1984.

Forb dynamics

Forb seed production occurred in each trapping site during the drought just after the two singular storms in November 1981 (before the study commenced) and in March 1983. Following the rains, the forbs flowered and seeded extensively from December 1983 to May 1984. The number of forbs and thus seed production was considerably lower during the drought than after.

Grass dynamics

The grass community was the most dynamic of the three vegetation groups. The grass communities in both landscapes had recovered to a certain extent after the August 1981 burn due to the November 1981 rainstorm. It was the first substantial rain since the burn and it was also the last until March 1983. At the start of the study, severe drought conditions had prevailed for almost a year and grass biomass levels were low with 1 780 kg/ha in the MKN and 2 000 kg/ha in the ACW. Despite being early summer, the plants were dry and brown (Figure 9, Table 8). The grass biomass in both landscapes continued to decline

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significantly to a steady low in Sessions 3 and 4. Although, there was a slight return of the grass to green conditions and limited inflorescence after the March 1983 rainstorm, this was of short duration.

Table 8: Mean grass biomass (kg/ha) [S.E] and its coefficient of variation (%) during the six trapping sessions in the MKN and ACW landscapes of the KNP.

	MKN		ACW	
Sessions	kg/ha	%	kg/ha	%
1	1778 [37]	27	2000 [61]	40
2	1879 [48]	33	1678 [58]	45
3	1526 [42]	36	1277 [57]	58
4	1574 [52]	43	1468 [60]	53
5	3473 [70]	26	3259 [113]	45
6	3887 [60]	20	2986 [121]	53

In three out of the four drought sessions, the mean grass biomass levels in the two landscapes were statistically different. Due to the large sample sizes taken in each habitat (168 trapsites in MKN and 170 in ACW) even relatively small differences can prove statistically significant and in the present study, I would consider that the different biomass means to be of doubtful biological significance.

During Session 4, the grass started turning green as the good rains began but inflorescence did not occur until a few weeks later, with seeding occurring soon after Session 4. During the 3 month interim between Sessions 4 and 5, the grass biomass in both landscapes increased by 120% and showed unlimited inflorescence. Despite the species and structural differences between the grass communities outlined earlier, the grass community responses to the drought and subsequent rains were nearly identical until Session 6 (Fig. 9). The difference in the grass biomass at that time was almost 1 000 kg/ha. In the MKN landscape, the grass biomass continued to increase significantly to 3 890 kg/ha while in the ACW, the grass biomass declined, however, it was not statistically significant (3 260 to below 3 000 kg/ha, t=1,64). This mean decline actually obscured the differential grass responses in the grassland, woodland and open vlei areas. The grassland patch grasses continued to increase as in the MKN but the woodland grasses were dying back while the vlei grasses were almost non-existent again. Thus the mean decline in the ACW grass biomass was not a uniform response as was the mean increase in the MKN.

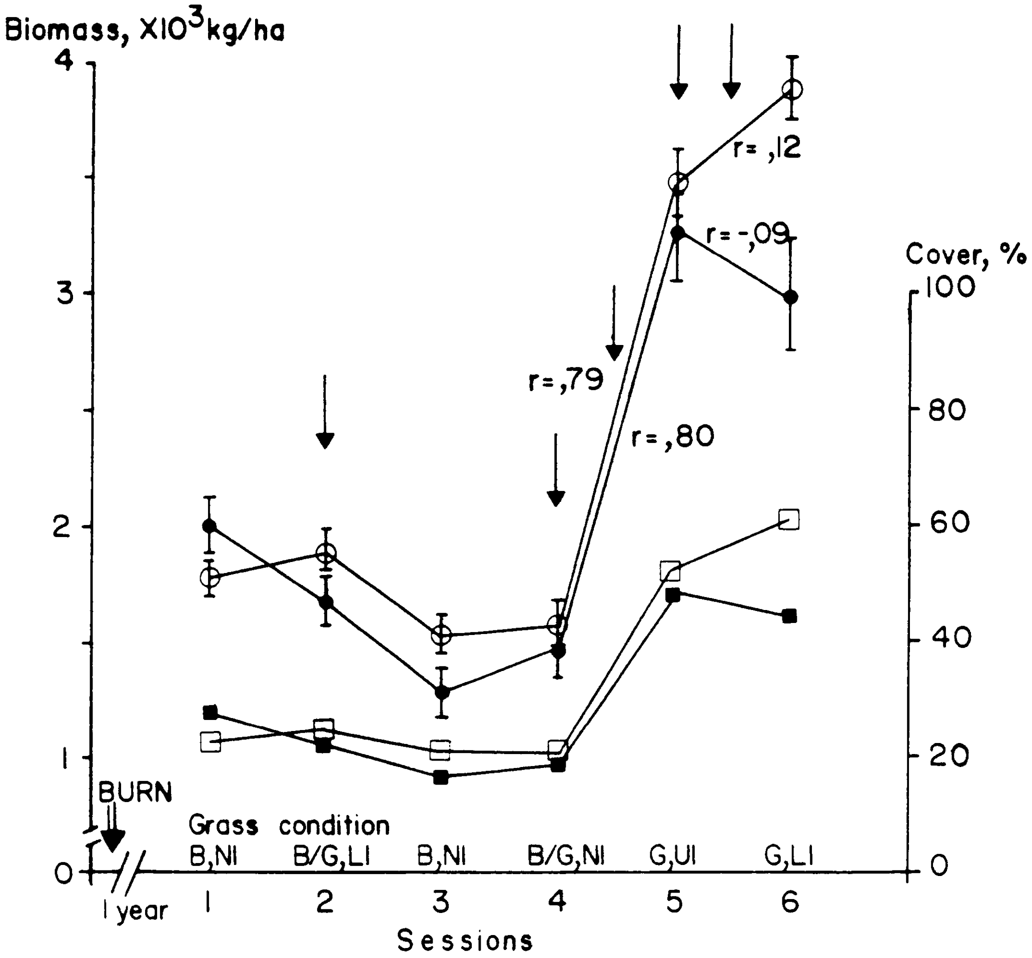

Figure 9: Mean grass biomass (kg/ha) with 95% c.l. (●,○), percentage grass canopy cover (■,□) and grass condition in the MKN (open symbols) and ACW (closed symbols) landscapes of the KNP. Grass condition is represented by B- brown, G- green vegetative parts and NI- no inflorescence, LI- limited and UI- unlimited inflorescence. ↓ > 50 mm of rainfall.

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The coefficients of variation (CV) associated with each grass biomass mean indicated how homogeneous the grass community structure was. The ACW CVs were consistently higher than those in the MKN (Table 8). The CVs in the MKN increased as the drought progressed showing that the grass plants were deterioratiing at different rates thereby producing a wider range of biomass estimates. Once the grass community began to recover, the MKN CVs immediately decreased as the grass layer once again became a uniform mat. In the ACW the CVs were high and variable throughout both the drought and rain periods. Thus the heterogeneity in the ACW grass community was a perpetual phenomenon and not a product of the environmental conditions as in the MKN The MKN, even during the drought, maintained a more homogeneous grass layer than the ACW.

The mean percentage grass cover hovered around 20% in both landscapes throughout the drought period (Figure 9). In the three months following the start of the rains, cover increased from 20% to about 50%, an increase of 150%. By Session 6, mean cover in the ACW had dropped slightly but was essentially the same whereas in the MKN, it continued to increase to above 60%. The sixth session increase in cover in the MKN represented a general increase throughout the sites but as with grass biomass, the slight decline in mean grass cover in the ACW obscured the different responses in the three patch types.

DISCUSSION

Species composition and relative abundance are controlling factors in vegetation community structure. Each species has its own unique growth form, reproductive pattern and potential. These species-specific characters influence many factors relevant to small mammal existence, such as the availability of ground cover, nesting sites, and food quantity and quality. Plant species and structural composition therefore, are an important defining element at both the macrohabitat and microhabitat levels.

The vegetation communities of the two sites within each landscape were sufficiently similar to enable a generalised description of each landscape to be made.

The MKN landscape is a low diversity, highly homogeneous, mono-level macrohabitat. The grass layer is well developed and covers the entire area. Although there are numerous trees and tree species, over 80% of them are less than 1,0 m. The emphasis on low height and low structural diversity overall results in the grass-level vegetation zone becoming the dominant feature of the macrohabitat. High species dominance, especially in the grass community, also contributes to the highly homogeneous state. Under favorable environmental conditions, the macrohabitat offers a minimum of microhabitat possibilities. Only under the severe drought conditions, when the grass plants had degenerated, did the general heterogeneity in the grass layer increase thus possibly increasing microhabitat options. Once the rains returned, the grass layer quickly increased homogeneity while the primary production and percentage grass cover continued to significantly increase throughout the rest of the study.

The ACW landscape could almost be considered as three macrohabitats. Each patch type, the grassland, woodland and vlei, have vegetation characteristics unique unto itself. However, because of the variable patch sizes (never encompassing more than 10 traps in any one uninterrupted stretch), their interspersed locations and the numerous non-classifiable inter-patch gradations, the three patch types, themselves, are one of the main characteristics of this macrohabitat. The patch types work together to form a complex macrohabitat which has extremely varied conditions. Plant species and structural diversity are high but because these vary within patch types, the macrohabitat is also highly non-uniform. The ACW is characterised by two distinct vegetation zones, the grass level including small trees within it ($\leq 0,5$ m), as in the MKN, and a definite tree foliage zone ($>1,0 \leq 4,0$ m). The two vegetation zones create a vertical as well as horizontal aspect in the macrohabitat. Although heterogeneity within the grassland patches changed with the climatic conditions as the MKN grass community did, the overall heterogeneity in the ACW grass layer was not altered greatly by either the drought or rain period. Thus the habitat had an inherent and stable heterogeneity which would maintain to some extent variety in the microhabitats available.

While the grasses in all three patches initially increased biomass after the rains, the late post-drought responses were quite different. The overall mean decline in the grass biomass between Sessions 5 and 6 was probably caused by three interrelated factors. First, the three patch types offered quite different micro-environmental conditions which may influence grass growth and survival (Langer 1979). The grassland patches had a well established grass layer, the woodland areas produced high shading effects and the vlei areas had periodically disturbed ground with total exposure to the elements. Secondly, the larger herbivores preferentially graze the ACW grass community (Gertenbach 1983), presumably because of the numerous palatable species. The dominant grass species in the MKN areas was _Bothriochloa radicans_ while in the ACW grassland patches there was co-dominance by _B. radicans_ and _Cymbopogon excavatus_. Both of these species are generally regarded as unpalatable by agronomists (Lightfoot 1970, Tainton, Bransby & Booysen 1978) and therefore would not be grazed much. However, some of the dominant species in the woodland and inter-patch areas of the ACW, such as _Panicum_ sp., _Themeda triandra_ or _Enteropogon monostachys_ are readily eaten (Lightfoot 1970, Tainton _et al._ 1978). Therefore there may have been differential grazing pressures on the three patch types, depending on the relative abundances of palatable grass species. Thirdly, each patch type tended to have its own unique grass species composition and all species tended to react to changing environmental conditions similarly. That is, species which grow under similar micro-climatic conditions also have similar life history patterns and requirements, such as the amount of energy needed and the amount of material put into the vegetative parts or the length of time the above ground plant parts survive. For example, a large energy input into vegetative parts may be highly advantageous in a grassland habitat where there is plenty of light for energy producing photosynthetic activities but in a woodland area, where light is limiting and high shade predominates or in arid conditions where water may be limiting, energy allocation may be best spent in quick seed production rather than vegetative production (Brown, Reichman & Davidson 1979, Langer 1979). These three factors affecting the ACW grass community would all ensure a non-uniform response by the grass community and thus a heterogeneous environment.

How can these macrohabitat features actually affect the small mammal communities? Plant species richness and species dominance can greatly affect both the variety of plant growth forms and also the potential food choices. High species dominance can result in a highly homogeneic environment whereby the immediate microhabitat is not only extensive and uniform but also fairly predictable. This is probably most important in terms of cover where known safety refuges are necessary for survival but, also because the plants can act as shelters for wind blown material, the soil seed reserves are generally significantly higher under plants and thus the predictability of food supply may be greater (Nelson & Chew 1977, Reichman & Oberstein 1977, Brown _et al._ 1979).

The virtually monospecific grass layer in the MKN was dominated by _Bothriochloa radicans_, a genus well known for its dense and uniform sward production (Lightfoot 1970, Tainton _et al._ 1978). Cover offered by this species would be highly predictable and it would offer a good collecting site for wind blown food. In the ACW, species richness is high, dominance is low and the grass layer is non-continuous. This heterogeneous state would reduce the predictability and availability of cover but by doing so would also enhance the creation of different microhabitats. Although unpredictable overall, cover may be fairly predictable within the grassland patches but patch sizes would limit it's extent. The predictability of food, however, would probably be unaltered as it would still be greater at the base of plants (grasses and trees), although this would be linked somewhat to the spatial distribution of the vegetation.

Species richness and species dominance also affect the potential food supply. If the diversity of food producers is low then the diversity of the food supply will also be low. I would speculate that the food provided by the grass layer in MKN would consist largely of _B. radicans_ seeds and, because of the density and distribution of the parent plants, these would be abundant and uniformly distributed. Moreover, Bothriochloa insculpta, a closely related species, has not only early and late flowering / seeding peaks but also a prolonged and sustained flowering period (Gibbs-Russell 1983), a trait apparent in B. radicans (pers. obs.). This would result in a more continuous seed input into the food supply.

Trees likewise provide a definite food source for small mammals (Watts 1969, Hansson 1971, 1984, Gashwiler 1979, Hornfeldt, Lofgren & Carlsson 1986). In the MKN, the dominant tree species were Dichrostachys cinerea and Acacia nigrescens and so these species should represent the greatest proportion of the tree seed food potential. However, most of the trees in the MKN were less than 1,0 m which is small for both species. I would suggest that most of the individuals were actually very young trees. Because of this, they may not have produced large quantities of seeds thus their real food input for the small mammals may have been quite limited.

The diversity of food types provided by the plant community of the ACW is probably quite high. The grass layer has a high species diversity but is far less extensive and in some places almost non-existent. This prompts three speculations about the small mammal food source. First, the interrupted grass layer in the ACW may produce less seed than the well developed grass layer in the MKN. Secondly, the food may be distributed as unevenly across the macrohabitat as the grass plants are. And thirdly, there may be increased exposure of the seeds in the ACW which get deposited or dispersed to areas outside the established grassland patches to both weathering and other seed predators or consumers.

The trees in ACW could provide a substantial number of seeds. The well established woodland areas, higher density of trees in general and their more even distribution may be very important to the food supply especially in view of the possible limitations of the grass layer. If the speculations about non-uniform distribution and exposure of the food supply in the ACW are true and apply to the tree seeds as well, then this could greatly affect the food reserves in particular types of microhabitats which could be a limiting factor in the existence of some small mammal species.

The consequences of the specific structural composition in each macrohabitat would be most apparent in the creation of microhabitats. Increased structural diversity, especially the establishment of a developed tree foliage zone, creates an additional dimension to the macrohabitat. A vertical dimension can be as important to a small mammal's survival as the horizontal one. Trees can be involved in predator avoidance strategies, nest site selection, and even food storage opportunities, however, they could also provide increased cover possibilities for the predators, especially birds of prey.

In addition, a high structural diversity can have a profound affect on the horizontal dimension. The competitive interactions of grasses and trees are well known (Barbour, Burk & Pitts 1980). Trees, especially when densely associated in a woodland, often limit grass growth through competition for light (shading effect), water and other essential nutrients (Hunt 1978, Langer 1979). In quantifying these macrohabitats, the interactive role of the tree and grass communities was very obvious. The higher density and often clumped association of the trees in the ACW created a variety of disruptions in the grass layer. These ranged from small bare patches beneath single trees to large expanses of sparse grasses under the woodland canopies. Trees in the MKN, though often the same species as in the ACW, were never closely associated and generally small. However, the larger species such as the Maroela tree (Sclerocarya caffra) had sufficiently open canopies for the shading effects to be minimal and the larger trees produced almost no disruptions in the uniformity of the grass layer.

The vegetation community structure analyses suggest that the MKN had a limited diversity of microhabitats which covered large areas where food and cover were probably fairly predictable. The ACW, on the other hand, had numerous microhabitat possibilities but with definite size limitations.

Changes in some of the vegetation parameters, such as primary production, can greatly affect both cover and food availability. These changes usually occur on a regular seasonal basis, however, in the first year of the present study, most of the seasonal variations were either absent or confounded by the effects of the drought.

The effects of drought on the availability and predictability of cover generally would occur slowly and mainly within the grass layer. As the grass leaves die, they lose their resiliency, become brittle and tend to break off (Hunt 1978). The cover offered by these vegetative parts becomes increasingly sparse. As the vegetative parts are lost, the nature of the cover changes from an aerially mediated cover to a basally mediated cover. That is to say, the reality of the cover changes from a hiding under to a hiding behind phenomenon. Under these circumstances, the spatial distribution of grass plants becomes increasingly important. A fairly even distribution of plants would assure a certain amount of spatial predictability to the cover. This was probably the case in the MKN. Although the grass cover was very low, the grass clumps, mostly just stems, were evenly distributed across the trapping sites. Despite the prolonged low cover situation induced by the drought, cover was still frequently available and reasonably predictable, however, the effectiveness of this as cover is unknown. In the ACW, cover predictability was probably reasonable only in the grassland patches and even there, the limited size and irregular patch boundaries reduced its extent. During the drought, there was no grass cover in the woodland or the vlei patches.

After the rains, cover in the MKN was not only predictable but also very uniform in most places. However, with greater uniformity, there were also fewer microhabitat possibilities. Cover in the ACW was also greatly increased but was still limited by the situations in different patch types and sizes. Numerous microhabitats with a broad range of cover situations were still available.

Another consequence of the prolonged drought conditions would be felt in the food supply. Soil seed reserves are generally replenished each year by grass, forb and tree seed production. The burning of the trapping areas in August 1981 could have substantially reduced the above ground availability of seeds. The fact that this coincided with the start of the drought was an additional hardship. Grasses and forbs were seen to produce limited amounts of seed in November 1981 and March

1983. Trees, however, last produced seeds between April and June 1981. Pulliam & Brand (1975) suggested that a year of low rainfall could precipitate a food crunch for not only the rodents but also, other seed predators, such as birds and ants, if all three groups were active. Similar results and conclusions have been presented in other studies (Davidson, Inouye & Brown 1984 and references therin). Non-small mammal trap captures during the drought showed that all three groups were active in the present study. Thus the food supply present in the soil could have had a lowered availability during the drought because of the fire, non-replenishment due to a lack of primary production and intense competition from other taxa. Following the rains, grasses and forbs produced seeds which seemed available to the small mammals within three to four weeks. Tree seeds, however, were essentially not replenished for the small mammals throughout the entire study period.

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CHAPTER FOUR

SMALL MAMMAL COMMUNITY STRUCTURE AND DYNAMICS

INTRODUCTION

An understanding of how small mammals are influenced by their biotic environment can only be acquired by analyzing changes in community composition, species diversity and species density as seasonal and climatic changes occur.

Species diversity of small mammals and species densities can be influenced by a maze of direct and indirect pathways. Abiotic factors such as rainfall, substrate, and temperature regimes indirectly influence small mammal communities through their influences on habitat complexity (Rosenzweig & Winakur 1969, Feldhamer 1979), primary production (Brown, J.H. 1973, Whitford 1976) and plant diversity (Hafner 1977). These factors in turn determine microhabitat availability, food and cover, and allow inter- and intra-specific competition to influence community dynamics (Goertz 1964, Watts 1969, Hansson 1971, Grant 1972, Birney, Grant & Baird 1976, Meserve 1976, Price 1978, Taitt & Krebs 1983, Anthony, Niles & Spring 1981, Parmenter & MacMahon 1983, Brown & Munger 1985, Spencer & Cameron 1985, Bowers 1986).

The two landscapes, MKN and ACW, were shown to have soil (Chapter 2), and certain vegetative and physiognomic differences (Chapter 3) which could be expected to influence the small mammal communities. Moreover, the climatic conditions during the study period were such that two highly distinct climatological periods, the drought and post-drought, were identifiable, both in rainfall pattern and vegetation dynamics. Using live-trapping and mark-recapture procedures, the small mammal communities were sampled to determine and then compare species diversity, small mammal density and biomass, community growth rates and estimates of maximum stable density (carrying capacity) between habitats and climatological periods.

The emphasis of this chapter is on the community responses of the small mammals. Individual species responses are dealt with in the following chapter. The small mammal community was comprised of both rodent, shrew and elephant shrew species which are taxonomically and ecologically very different groups of animals. As it is possible that they could respond in different ways to the environmental changes, analyses of community size and growth were carried out separately for these two groups.

METHODS AND MATERIALS

Live-trapping Programme

Before the start of the study, a preliminary live-trapping exercise was conducted from August to October 1982, to ascertain the status of the small mammal communities. The small mammal numbers and trapping success were very low while the mean distance between captures was quite high (Table 9). These results, which suggested that the animals were at very low densities and widely dispersed, and the fact that only a limited number of traps were available for the study greatly influenced the choice of trapping methods used in the live-trapping programme.

To maximise small mammal encounter rate and adequately sample the variety of microhabitats present in the ACW, the trapping configuration had to intersect as many small mammal home ranges and microhabitats as possible, therefore, census lines rather than a grid were chosen. Two permanently marked parallel census lines, 50 m apart, with 20 m between trap stations, were set up on the two trapping sites in each habitat. One hundred Sherman folding live-traps (270x77x90 mm) were available for the study. However, due to interference by larger mammals (see Watson & Watson 1985), it was necessary to retain a few spare traps for replacement of lost or damaged traps. Initially, 90 traps, 45 per line, were set out each night of trapping but as some traps were unavoidably lost and a number of traps had to remain spare, only 84 traps, 42 per line, were set out by the end of the study.

Each trapping site was censused six times with trapping sessions being held three times per year in early summer

(November/December), late summer (March/April), and winter (July/August). These three periods are demographically important to southern African small mammals as they represent the start and end of the breeding season, early and late summer respectively, and the non-breeding season.

Table 9: Preliminary small mammal trapping results from areas in their first and third years after burn in the MKN and ACW landscapes of the KNP. *, ** and *** list the species and number of each species () captured. *- Saccostomus campestris (5), Tatera leucogaster (1), Praomys sp. (1), Steatomys pratensis (1). **- S. campestris (1), T. leucogaster (1), Lemniscomys griselda (1), Mus minutoides (2), Aethomys chrysophilus (1). ***- S. campestris (4), L. griselda (1), A. chrysophilus (1), Dendromus mystacalis (1). ^{a}- two trap-habituated animals accounted for 10 out of 18 captures.

	MKN	ACW	
Year after burn	1	1	3
No. Species	4*	5**	4***
No. Individuals	8	6	7
No. Captures	15	18^{a}	13
No. Trapnights	793	321	731
% Trapping Success	1,9	5,6	1,8
$\bar{x}$ distance between captures	215	407	293

Traps were set for nine consecutive nights in each trapping site. Although this was relatively long, it was considered necessary because the wide dispersion of the trapping configuration (20 m between traps, 50 m between lines) meant the chances of a small mammal encountering a trap every night were low. In Session 6, traps were set on the regular traplines for only 6 nights because 3 nights of assessment line trapping (O'Farrell, Kaufman & Lundahl 1977, see population estimations below) had to be incorporated into the trapping schedule.

In the MKN areas, from Session 2 to Session 4, black-backed jackal (Canis mesomelas) disturbance of the traps was an increasing problem. In Session 4, trap depredation was highly successful and trapping in M1 was stopped two days early to prevent further loss of life while in M2 trapping was interrupted for one week while trap protectors were devised. The protectors were 100% effective against jackal depredation and did not influence the small mammal capture rates (Watson & Watson 1985). All subsequent trapping in the MKN areas was undertaken using the trap protectors.

Due to the limited number of traps, trapping in the four sites occurred sequentially rather than concurrently. This resulted in 36 consecutive nights of trapping which unavoidably intruded into the full moon phase of the lunar cycle. As high intensity moonlight is known to inhibit small mammal activity (Clark 1983, Kotler 1984a, 1984b and references therein), trapping was not conducted during the four nights either side of the full moon. Thus the trapping session took 45 nights to complete with the trapping schedule standardised in the following order: M1, A1, full moon phase (9 nights), M2, A2. There were about 60 days between trapping sessions and 90 days between trapping at any one site.

Traps were checked each morning and rebaited daily with a mixture of peanut butter and rolled oats. Traps could not be checked at night due to the dangers of nocturnal encounters with some of the larger mammals. Initially, diurnal trapping was also conducted, however, as only squirrels, which were not included in this study because on the whole they were too large for the available traps, and birds were captured, this trapping was stopped. During each morning check, all occupied traps were collected and cleaned under running water before replacement in the field that afternoon. This procedure was followed to eliminate the odours of the previous occupant which other studies have often shown can influence the trap's next captive and create biases in the trapping results (Summerlin & Wolfe 1973, Boonstra & Krebs 1976, Daly, Wilson & Behrends 1980, Stoddart 1982, Wuensch 1982, Daly & Behrends 1984).

Trap-habituated animals can also influence population statistics by monopolising certain traps. To limit this problem, any trap which caught the same individual for two consecutive nights was removed for one night to allow the animal to forage in other areas of its home range.

To prevent an under-estimation of the trapping success, any trap which was removed because of trap-habituated animals, closed without a captive, had a non-small mammal captive or was disturbed and/or damaged by non-study animals was disregarded in the calculation of the number of trap nights.

Recorded Data

The small mammal censusing programme was conducted using mark-recapture and toe-clipping procedures. Upon capture, the following data from each captive were recorded: species, toe-clip number, mass, relative age, sex, breeding condition and the trap station number.

The 13 small mammal species captured were generally easily identified with careful visual inspection, however, two species, *Praomys coucha* and *Praomys natalensis* were impossible to tell apart in the field. To identify these animals, a small blood sample was collected in a capillary tube, then sealed, labelled and frozen for later electrophoretic analysis of the blood proteins (see Gordon & Watson 1986 for methodology). Analysis of the blood samples and identification of the *Praomys* individuals to species were determined after each trapping session.

Mass was obtained using either a 100 g or 300 g Pesola spring balance. Mass records for individuals captured on numerous occasions were averaged and then species means were calculated in each session.

Relative age classification was based on mass measurements and pelage colour. As this chapter deals broadly with the small mammal community dynamics, the species specific mass/aging criteria are dealt with in more detail in the following chapter and there are summarised in Table 18.

Sex and breeding condition were determined by external sexual/ reproductive characteristics. Males were declared breeding if scrotal testes were evident and females if they had a perforate vagina, vaginal plug or were obviously pregnant or lactating. Reproductive condition of the shrews was generally impossible to determine for live animals and so this information was not obtained. After all the relevant data were recorded, each animal was released at the point of capture.

Community Analyses

Species composition

All diversity and evenness indices were calculated using the Shannon's diversity (H', J') formulae (see Chapter 2). Differences between the diversity values were tested for significance at the $P<0,05$ level, using Hutcheson's t-test (Zar 1984). Community similarity was calculated using Sorensen's modified index of community similarity (C_N) (Southwood 1978, see Chapter 2).

Population estimation

Choosing an appropriate mark-recapture model for the estimation of small mammal population size is very important but also highly problematical. Blending a model's inviolable assumptions with the reality and limitations of data gathered from a naturally occurring population in a non-controlled environment inevitably leads to some compromises. The five basic assumptions (De Blase & Martin 1981) which most mark-recapture models demand are:

1. Animals do not lose their marks.
2. Animals are correctly recorded as marked or unmarked.
3. Marking does not alter the probability of the marked animal's survival.
4. The population is recognised as closed (no gain or loss of members during the sampling period) or open (gain and loss of members occurs but affects marked and unmarked animals equally) depending on whether a deterministic (closed) or stochastic (open) model is chosen.
5. The marked animals disperse randomly in the population and that all members have an equal probability of capture.

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Numerous considerations had to be taken into account when choosing the population estimation model for use in this study. A stochastic model, such as the commonly used Jolly-Seber method (Jolly 1965, Seber 1965), was considered inappropriate because of the relatively long inter-session trapping intervals compared to the lifespan and residency period of most small mammals and the very low numbers of small mammals present at the start of the study. All of which would reduce the probability of individual recaptures in sequential trapping sessions (Seber 1973, Southwood 1978, Begon 1979). Under low density conditions, the simpler deterministic models are often less biased estimators (Menkens & Anderson 1986). Among the deterministic models, the Schumacher model (Schumacher & Eschmeyer 1943) was more suitable than the Schnabel (1938) method as it is easier to compute (De Blase & Martin 1981), is explicit as opposed to iterative (Caughley 1977), and is less dependent on random mixing of marked and unmarked animals (De Lury 1958), an unlikely occurrence if territoriality functions in the community (Eberhardt 1969). The Schumacher model was also preferable to the Peterson Index as it allows a longer marking period which would increase the numbers captured and marked and has the added advantage of allowing a check on the assumption of equal catchability, which is the most often violated assumption of the mark-recapture models (Caughley 1977). Population size calculated by the Schumacher model uses the following equation:

$$N = \sum M_i^2 n_i \, / \sum M_i \, m_i$$

where N is the population estimate, M_i is the number of individuals marked prior to the ith occasion, n_i is the number of individuals captured on the ith occasion and m_i is the number of previously marked individuals in n_i. The standard error of N is calculated indirectly by first computing the standard error of 1/N which is:

$$s \, / \sqrt{\sum M_i^2 \, n_i}$$

where s is calculated from:

$$s^2 = \frac{\sum_{j=1}^{J}(m_i^2/n_i) - (\sum M_i \; m_i)^2 \; / \; (\sum M_i^2 \; n_i)}{J - 1}$$

and J is the number of trapping days. The 95% confidence limits of N are obtained by inverting the 95% confidence limits calculated for 1/N (that is the standard error of 1/N times the P<0,05 t value for J-1 degrees of freedom) (Caughley 1977).

The check on equal catchability is made by regressing M_i/n_i on M_i. The resulting linear equation should go through the origin and have a slope of 1/N (Caughley 1977). The assumption of equal catchability has been violated if the resulting equation differs significantly from the equation $Y = 0 + (1/N)X$.

Population size estimates for each habitat were made by pooling the mark-recapture results from the two trapping areas in each habitat. Because the capture and recapture of shrews was extremely low, use of a mark-recapture model was inappropriate and therefore, size of the shrew community was taken as the number of individuals captured in each habitat.

For realistic comparisons of community size, population estimates were converted to density estimates, that is the number of animals per hectare (a/ha), by determining and then dividing by the trapping area. The effective area of trapping, however, is usually larger than the area covered by the trapping configuration because of small mammal mobility and the attraction of baits (Smith, Blessing, Chelton, Gentry, Golley & McGinnes 1971, O'Farrell _et al._ 1977, Wilson & Anderson 1985). Small mammal mobility is known to vary with density, home range size, season, and heterogeneity of the environment (Sanderson 1966, Rosenzweig & Winakur 1969, Smith _et al._ 1971, Kenagy 1973, Wolff 1985b), therefore, the effective trapping area must be estimated for each period and location of trapping. Calculation of the additional area of trapping (W_a) (i.e. the area beyond that covered by the census lines from which animals may have come) was made using the mean maximum distance moved (MMDM) method (Grant, French & Swift 1977, Wilson & Anderson 1985) but with the

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distances first being adjusted to include half the distance to the next trap (Stickel 1954). Only capture records of resident animals, those captured three or more times in any one session or captured in more than one session, were averaged together for the W_a value. For example, if seven animals, who fulfilled the residency requirement, travelled maximum distances of 90, 30, 50, 64, 10, 50 and 54 m, the mean maximum distance moved or W_a was 87 m. Adding this then to the length (960 m) and width (50 m) of the census lines yields a total trapping area (A_t) of 14,3 ha. A_t (±95% c.l.) was calculated for each trapping area individually and then combined for each habitat's A_t.

Due to the low capture and recapture rates of shrews, A_t could not be calculated and so trapping area was considered simply as the area covered by the trapping configuration.

The MMDM method of W_a assessment relies on an adequate number of traps being available for small mammal capture throughout the night. If trapping success is very high (Gurnell & Flowerdew (1982) suggest >70%), it is inevitable that some animals will be refused entry due to occupied traps and thus, MMDM may not be a true reflection of the distances a small mammal may travel. In Session 6, the MKN mean trapping success rate was 94%, however, as there were no more traps available to be put out, little could be done to counteract the consequences this would have on both the population size and A_t estimations. For this reason, the assessment line technique (Smith et al. 1971, Kaufman, Smith, Jones, Gentry & Smith 1971) for parallel census lines (O'Farrell et al. 1977) was used to provide additional estimates of N and W_a. For three nights following the six nights of normal mark-recapture procedures, the traps were repositioned at 10 m spacings along three equidistant lines intersecting the previous census lines at a 45^o angle (Fig. 10). All animals caught on the assessment lines were recorded as either marked or unmarked and their distances along the assessment lines noted. The perpendicular distance of a trap from the census lines was determined using the Pythagorean's theorem for calculating the length of the legs of a right triangle. This is best explained using an example (refer to Fig. 10). If the farthest a marked animal was captured on one assessment line was trap 6, the distance C = 6 X 10 m spacing + 5 m (half the interstation trap distance) = 65 m. Pythagorean's theorum states that $C^2 = A^2 + B^2$ where, for a right triangle, A = B, therefore, $(65)^2 = 2A^2$ and thus A (or W_a) = 46 m. However, due probably to habitat heterogeneity, the maximum distance moved by the small mammals along each assessment line was not constant. To avoid overestimating the area of effect, the mean maximum W_A, in this case the perpendicular widths, for the six assessment lines was calculated. The calculation for the total area of trapping effect is:

$$A_t = L_W L_L + 2L_L W_A + \pi r^2$$

where L_W and L_L is the width and length respectively of the plot encompassed by the parallel census lines and r is W_A plus half the distance between the census lines (O'Farrell _et al._ 1977).

Once the total area of effect is calculated, the ratio of marked animals to total animals caught on the assessment lines (R_p) is calculated as:

$$R_p = M / T$$

where M is the number of marked animals captured and T is the total number caught on the assessment lines within the W_a. The estimate of the number of animals within the A_t (N_A) then is:

$$N_A = N_G / R_p$$

where N_G is the total number of animals marked during the regular mark-recapture procedure. Density is then estimated as:

$$D = N_A / A_t$$

Confidence intervals were not calculated for this estimate as this would have entailed the running of simultaneous replicate plots (O'Farrell _et al._ 1977) and sufficient traps and time were not available.

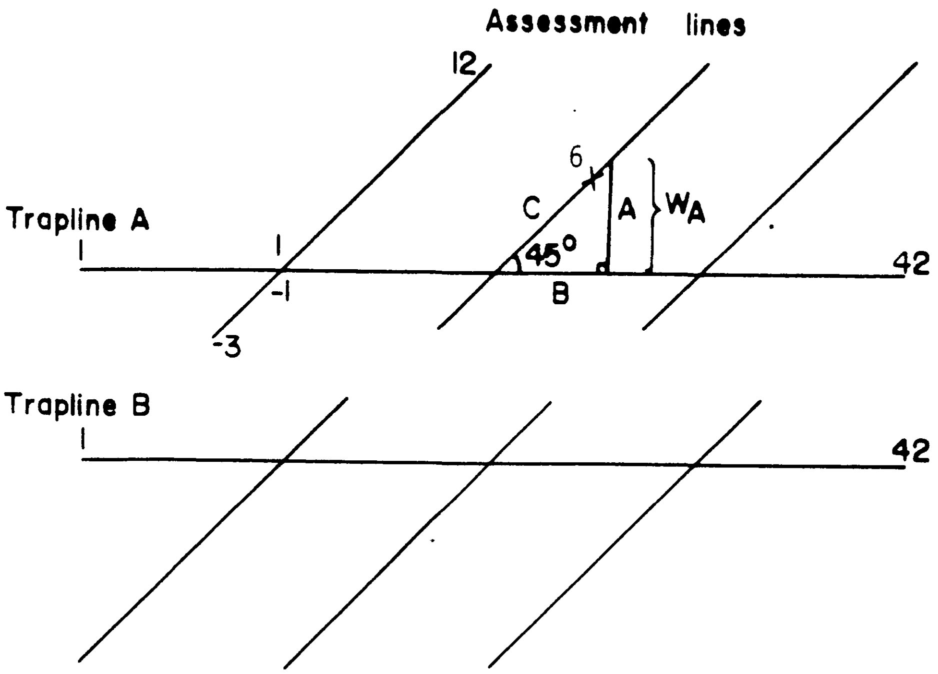

Figure 10: The two parallel trap lines, A & B, with 42 traps and 20 m spacing per line. The trap lines are intersected at 45° angle with six assessment lines, each with 12 traps (1 to 12) outside the lines and 3 traps (-1 to -3) inside the lines at 10 m spacing. X marks trap 6, a perpendicular line is drawn from the assessment line trap (+ 5 m, half the inter-trap spacing) to the trap line to form right triangle ABC. Distance C then equals 65 m. (Figure not drawn to scale)

Rates of population increase over time are an indication of the population's demographic vigour. Three correlated measures of increase are recognised, however, only two, the observed rate ($\bar{r}$) and the intrinsic rate (r_m) are used in this study. Both $\bar{r}$ and r_m are exponential rates of increase over time. The distinction between the two is that r_m assumes that the rate of increase and the age distribution are constant and that the resources are in super-abundance, while $\bar{r}$ does not (Caughley 1977). According to these assumptions, then r_m is determined by the population's genetic constitution while the $\bar{r}$ shows the results of interactions with the quality of the environment. The $\bar{r}$ was calculated over the drought and post-drought sessions using the equation:

$$\bar{r} = \frac{\sum_{i=1}^{t} N_i t_i - (\sum N_i)(\sum t_i)/n}{t_i^2 - (\sum t_i)^2/n}$$

where N_i is the natural logarithm of the density in Session i, t_i is the sampling period (i.e. Session 1, 2, 3 . . .) and n is the number of density estimates (Caughley 1977). Calculations of r_m require survival and fecundity schedules which were not obtainable with my methods of data collection. While r_m was not calculated directly, it is discussed in relation to the $\bar{r}$ values based on distinctions between the definitions of the two values.

If the population growth curves are modelled using the logistic model (Morista 1965), the point of stable equilibrium of density or namely a habitat's carrying capacity (K) can be predicted. During logistic growth, the trend of $(N_{t+1}-N_t)/N_t$ is linear on N_{t+1} such that $(N_{t+1}-N_t)/N_t = a-bN_{t+1}$ where $a = e^{r_m}-1$ and $b = a/K$. Thus K and r_m can be estimated using the least squares regression if at least three estimates of density are available (Caughley 1977). The rodent carrying capacity of the two habitats was estimated from the growth curves in the drought period, Sessions 1 to 4, and in the post-drought period, Sessions 4 to 6.

Where statistical analysis of comparisons of the various community parameters was appropriate, t-tests for equal and unequal variances were used. Significant differences were accepted at the $P<0,05$ level and in most cases, the 95% confidence limits are reported.

RESULTS

Small mammal trapping success in the MKN varied from a low of 4% in the drought sessions (1-4) to 94% in the post-drought sessions (5-6) (Table 10). Similar trends in trapping success occurred in the ACW, however, the maximum trapping success in the post-drought never exceeded 50%.

Table 10: Summary of small mammal live-trapping results from six trapping sessions in the MKN and ACW landscapes of the KNP. TN - number of trap nights, %TS - percentage trapping success, N_c - number of captures, N_m - number of marked individuals and N_s - number of species captured. ES, LS and W - early, late summer and winter season respectively.

	MKN					ACW				
	TN	%TS	N_c	N_m	N_s	TN	%TS	N_c	N_m	N_s
Session 1, ES Nov./Dec. 82	1636	4	71	35	4	1542	7	103	28	7
Session 2, LS Mar./Apr. 83	1395	10	145	54	7	1611	8	122	36	7
Session 3, W July/Aug. 83	1465	17	245	70	7	1572	7	110	36	10
Session 4, ES Nov./Dec. 83	1263	14	180	75	6	1383	10	141	51	7
Session 5, LS Mar./Apr. 84	1403	58	810	288	6	1359	40	541	199	7
Session 6, W July/Aug. 84	912	94	861	395	7	920	49	451	208	8

The lower number of trapnights in the MKN Sessions 2, 3 and 4 was due to the high level of interference by black-backed jackals, which accounted for numerous closed but empty traps. Trap depredation, however, only became efficient in Session 4, where the total number of captures (N_c) was lower than in Session 3, despite a greater number of anmals marked (N_m). This reflects the high loss of life at that time. Of the 75 animals captured, 45% were known to have been killed by the jackals. These events forced the interruption of trapping until an effective method of trap protection was devised (Watson & Watson 1985). Trapping was resumed but to maintain the trapping schedule such that full moon was avoided, two nights of trapping were lost. Following the introduction of the trap protectors, trapping effort in the two habitats again became similar as the number of trap nights in Sessions 5 and 6 show (Table 10).

The number of species present in each landscape was fairly consistent throughtout the study period (Table 10). The MKN had a maximum of seven species with a mean of 6,1 species present at any one time while the ACW had a maximum of 10 species with a mean of 7,4. There is no significant difference between the mean number of species present in the two habitats, however, overall the ACW showed the greater species richness.

Although there was a consistency in the number of species present in each trapping session, not all species were present each time. Over the entire study period, a total of 10 species were recorded in the MKN while 11 species were recorded in the ACW (Table 11). *Praomys coucha* and *Saccostomus campestris* were the numerically dominant rodent species in MKN habitat in both climatic periods. *S. campestris* was the only numerous species in the ACW during the drought, however, after the rains, both *P. coucha* and *S. campestris* were common. All other rodent species showed a low level or sporadic presence. Of particular interest is the total absence of *Aethomys chrysophilus* and the late arrival of *Praomys natalensis* in the MKN while *Aethomys namaquensis* was absent from the ACW. The MKN showed a numerically depauperate shrew community in comparison to that of the ACW.

While the numerical dominance of *P. coucha* and *S. campestris* in the two habitats made their population responses most obvious, the responses of most of the other species showed the same qualitative, if not quantitative, trends in the drought and post-drought periods, that is low numbers of individuals were caught during the drought followed by an increase after the rains (Table 11). However, the symmetry in the responses tends to breakdown in the last trapping session. In the MKN, most species

Table 11: Small mammal community composition andthe number of individuals captured in the MKN and ACW landscapes of the KNP. ES, LS and W as before. * - estimate of the number as not all _Praomys_ sp. individuals had blood taken. For further detailssee Chapter 5.

	MKN Sessions						ACW Sessions					
	Drought				Post-Dr.		Drought				Post-Dr.	
Small Mammals	1 (ES)	2 (LS)	3 (W)	4 (ES)	5 (LS)	6 (W)	1 (ES)	2 (LS)	3 (W)	4 (ES)	5 (LS)	6 (W)
Rodent Species												
Saccostomus campestris	22	22	29	28	83	3	14	23	16	36	99	16
Praomys coucha	6	19	32	29	174	366*	0	0	1	1	55	116
Praomys natalensis	0	0	0	0	0	8*	1	0	1	5	15	42
Tatera leucogaster	0	2	3	2	18	6	4	1	4	4	13	13
Aethomys chrysophilus	0	0	0	0	0	0	4	3	4	1	4	9
Aethomys namaquensis	0	2	2	3	1	8	0	0	0	0	0	0
Lemniscomys griselda	0	2	1	1	4	1	2	1	2	0	0	1
Steatomys pratensis	6	5	1	0	0	0	2	2	1	2	0	0
Mus minutoides	1	0	2	3	0	0	1	0	3	0	0	1
Graphiurus murinus	0	0	0	0	0	0	0	0	0	0	3	0
Shrew / Elephant Shrew Species												
Crocidura hirta	0	0	0	0	8	3	0	1	2	2	10	10
Elephantulus brachyrynchus	0	0	0	0	0	0	0	5	2	0	0	0
Crocidura bicolor	0	2	0	0	0	0	0	0	0	0	0	0

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again occurred only in low numbers while P. coucha increased as dramatically as S. campestris declined. In the ACW, the two Praomys species both increased while S. campestris declined, and all the other species maintained their increased numbers.

Species diversity of the ACW community was significantly greater than that of the MKN in four out of six trapping sessions (1, 3, 5 & 6) while there were no significant differences in Sessions 2 and 4 (Fig. 11, bar graph). Species diversity in the MKN during the drought sessions was fairly stable around 1,20, however, after the rains, diversity started to decrease markedly, such that by the sixth session it was only 0,41. Evenness in the MKN followed a gently decreasing trend throughout the study until the last session when it also declined markedly (Fig. 11, circles). This was due to the almost total dominance of P. coucha in the MKN at this time.

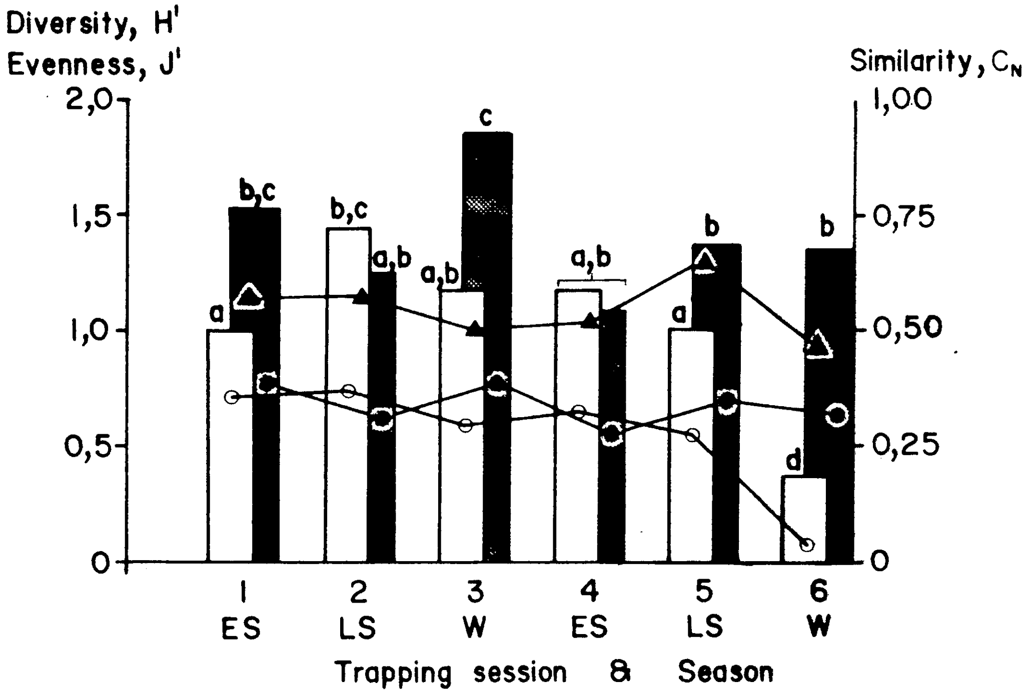

Figure 11: Bar graph of small mammal species diversity (H') with the evenness index (J')(○,●) and Sorenson's community similarity index (C_N)(▲) line graphs superimposed. Open symbols/bars denote the MKN and closed symbols/shaded bars the ACW landscapes. Bars with shared lower case letters are not statistically different ($P<0,05$).

In contrast to the MKN pattern, diversity in the ACW fluctuated rather erratically during the drought, however, in the post-drought period, it stabilised around 1,36. The erratic diversity in the ACW was also reflected in the evenness indices. In both indices, the erratic nature was due to the low numbers of individuals of each species captured rather than to big changes in species richness. Following the rains, however, all species in the ACW maintained sufficient numbers to stabilise the indices despite the dominance of P. coucha (Table 11, Fig. 11).

Similarity between the two small mammal communities in each session was generally stable throughout the drought period (Fig. 11, asterisks). It increased immediately following the rains, as all species increased in number but then declined sharply in the final session as P. coucha dominated the MKN community to a far greater extent than the ACW community.

While change in species composition is an important aspect of community structure and dynamics, equally important is change in the size of the community. Accurate determination of density depends on the accuracy in the assessment of size of the population and the area from which the animals were sampled. The general accuracy of the Schumacher model was substantiated by the remarkable closeness of most of the estimates (N_E) to the actual number marked (N_m) (Table 12). However, in two instances, doubts about the accuracy were raised. First, according to the Schumacher check on equal catchability, this assumption may not have been met in MKN Session 3 where the y-intercept of the equation $y=0{,}066+0{,}031x$ was significantly different from $y = 0{,}0$ at the $P<0{,}05$ level. This was probably due either to jackal depredations or a type I statistical error. However, because the y-intercept was only just significantly different and the N_m and N_E were so close, I find it reasonable to accept the Session 3 estimate as an accurate reflection of the true population size.

Doubt was also raised about the accuracy of the N_E in MKN Session 4, where the N_m exceeded even the 95% confidence limits of the N_E (Table 12). This inaccuracy could again be attributed to the jackal depredations, where at least 45% of the marked animals in that session were killed. This is a direct violation of the closed population assumption (the population is neither increasing nor decreasing during the sampling period) of the Schumacher model and therefore, the accuracy of the population estimate is very much in doubt.

Table 12: Small mammal community population estimates with a check on equal catchability for the MKN and ACW landscapes of the KNP. N_m - number marked, N_E - Schumacher population estimate [95% c.l.]. Lower case letters denote the $t_{(0,05,n-1)}$ value, where n = number of nights trapped, for determining 95% c.l. of slope and y-intercept. This will determine significant deviations of M_i/n_i on M_i (see text for definitions) from y=0+(1/N)x, the equation showing equal catchability. ^{a}=2,306, ^{b}=2,262, ^{c}=2,571, ES, LS and W as before. * - significant difference P<0,05.

Session	N_m	N_E	1/N	Linear Equation ($\pm$SE)
MKN				
1 (ES)	35	38 [29-55]	0,026	^{a}y= 0,206[0,109] + 0,0181[0,0071]x
2 (LS)	54	55 [50-61]	0,018	^{b}y= 0,085[0,062] + 0,0159[0,0018]x
3 (W)	70	69 [66-73]	0,014	^{b}y= 0,066[0,025]*+ 0,0133[0,0004]x
4 (ES)	75	52 [42-64]	0,019	^{a}y= 0,033[0,101] + 0,0189[0,0033]x
5 (LS)	288	282 [254-318]	0,003	^{a}y= 0,078[0,051] + 0,0032[0,0003]x
6 (W)	395	438 [402-481]	0,002	^{c}y=-0,015[0,018] + 0,0023[0,0001]x
ACW				
1 (ES)	28	26 [24-29]	0,039	^{a}y= 0,060[0,073] + 0,0363[0,0039]x
2 (LS)	36	33 [28-40]	0,030	^{b}y= 0,118[0,078] + 0,0256[0,0036]x
3 (W)	36	32 [26-42]	0,031	^{b}y= 0,131[0,131] + 0,0277[0,0067]x
4 (ES)	51	51 [42-64]	0,020	^{a}y= 0,165[0,089] + 0,0157[0,0031]x
5 (LS)	199	199 [175-229]	0,005	^{a}y= 0,095[0,052] + 0,0044[0,0004]x
6 (W)	208	210 [179-254]	0,005	^{c}y= 0,029[0,032] + 0,0046[0,0004]x

Because of the blatant differences between N_E and N_m and the known violation of one of the assumptions, a population estimate was attempted using the Jolly-Seber method which, being a stochastic model, allows for an open population where death or emigration can occur. The Jolly-Seber result before the jackal depredations (fourth night of the trapping session) occurred was 91 animals but with a 95% confidence interval of 20 - 162 animals. By the end of the trapping session, the Jolly-Seber estimate was 40 animals with 95% confidence limits of 7 - 73 animals. The exceptionally large confidence limits around both estimates is due to the low rate of capture and recapture samples each night. This problem is inherent in the stochastic models under such low population conditions (Menkens & Anderson 1986) and the accuracy of these estimates must also be treated with caution as the confidence limits suggest. In the absence of a reasonable population estimate, the actual number caught (N_m), that of 75 animals, is accepted as the most accurate estimate of the population size as it might have been without the jackal depredations. However, for the subsequent estimates of population increase, that is from Sessions 4 to 5 and 6, the number of individuals caught minus the number killed namely, 44 animals, was used as the initial population size.

The calculations of the total area sampled (A_t) in each session and habitat are presented in Table 13. The percentage of "residents" in each community and therefore, those that contributed to the calculation of the A_t was highly variable early in the study due to the low number of animals captured. However, as the study progressed, the number of animals contributing to the calculation of A_t stabalised between 40 and 50% of the captured population.

In most cases, the intra-habitat variation in the mean maximum distances moved by the rodents was relatively small (Table 13). The coefficients of variation for the MMDM values were high in both habitats throughout the study, however, as the numbers of animals increased, the variation in distances moved tended to be more consistent.

In Sessions 1, 2, and 6, the MMDM values in the trapping sites segregate nicely by habitat, however, in Sessions 3 and 5, MMDM values are most similar according to the pre- and post-full moon trapping times (Table 13). No pattern of small mammal movement according to habitat was discernible. Such a pattern might have been expected if the patch types in the ACW had affected the distance moved either as a result of restriction to a patch or extension by moving between patches. Neither the MMDM nor the A_t values followed any consistent site or habitat specific patterns.

Table 13: Mean maximum distance moved (MMDM [CV]) and the total area of trapping (A_t [95% c.l.] for the four trapping sites (MMDM method) and the rodent community population estimates (N_E, [95% c.l.], Schumacher method) in the MKN and ACW landscapes of the KNP. %R (n) - percentage and number of residents in the community. Lower case letters indicate length of the traplines for each site and session (width standardised at 50 m), a=960 m, b=920 m, c=900 m, d=880 m, e=860 m, f=840 m, *- population size based on numbers captured regardless of number of deaths. **- population size calculated by subtracting number killed from number captured (see text for explanation). ES, LS and W as before.

Session	Trap Site	%R(n)	MMDM(m)	Site A_t(ha)	Landscape N_E	A_t(ha)
1 (ES)	M1	18(3)	74^a[68]	12,8 [9,2-17,4]	38	26,2
	M2	39(7)	79^a[120]	11,8 [9,3-17,7]	[29-55]	[18,5-35,1]
	A1	61(8)	87^a[123]	14,3 [10,0-19,0]	26	28,8
	A2	53(8)	91^a[90]	14,5 [11,2-18,0]	[24-29]	[21,2-37,0]
2 (LS)	M1	32(8)	137^b[74]	19,8 [15,4-24,4]	55	40,7
	M2	51(15)	149^c[88]	20,9 [16,7-25,2]	[50-61]	[32,1-49,6]
	A1	68(13)	87^c[91]	13,5 [11,1-16,0]	27	26,0
	A2	29(5)	78^c[40]	12,5 [9,5-15,6]	[23-32]	[20,6-31,6]
3 (W)	M1	44(8)	59^d[58]	10,2 [9,0-11,5]	69	23,7
	M2	69(36)	89^d[81]	13,5 [12,2-14,8]	[66-73]	[21,2-26,3]
	A1	55(10)	58^d[65]	10,1 [8,9-11,4]	26	22,4
	A2	50(9)	76^c[118]	12,3 [9,1-15,7]	[20-32]	[18,0-27,1]
4 (ES)	M1	42(16)	118^d[88]	16,8 [13,8-19,9]	*75/44**	30,8
	M2	46(13)	96^e[94]	14,0 [11,3-16,8]		[25,1-36,7]
	A1	46(16)	97^d[107]	14,4 [11,5-17,4]	47	31,4
	A2	44(7)	123^e[80]	17,0 [12,9-21,4]	[38-60]	[24,4-38,8]
5 (LS)	M1	38(40)	53^e[60]	9,4 [9,0- 9,9]	273	18,0
	M2	43(80)	47^f[76]	8,6 [8,3- 9,0]	[244-308]	[17,3-18,9]
	A1	37(37)	59^f[52]	9,8 [9,3-10,4]	186	18,6
	A2	48(44)	49^f[68]	8,8 [8,3- 9,3]	[165-214]	[17,6-19,7]
6 (W)	M1	32(71)	22^f[77]	6,2 [6,0- 6,5]	434	12,3
	M2	40(71)	21^f[80]	6,1 [5,9- 6,3]	[398-476]	[12,1-12,8]
	A1	28(38)	35^f[70]	7,4 [7,1- 7,8]	207	14,4
	A2	43(31)	30^f[56]	7,0 [6,8- 7,2]	[179-246]	[13,9-15,0]

Aside from Session 2, where the overall MKN habitat A_t was much larger than the ACW (40,7 ha versus 26,0 ha respectively), the two habitats revealed remarkably similar A_t values throughout the study (Table 13). Comparing the overall habitat A_t values between sessions again did not reveal any consistent pattern except for a large decrease in all values as the numbers caught increased in the post-drought period. A simple correlation analysis of the numbers caught and the number of residents in each habitat with the MMDM and A_t values showed a significant negative correlation in both habitats (Table 14). Thus the strongest pattern revealed relates to community size and distances moved by individuals rather than any habitat specific feature, a relationship which many other studies have found (Brown 1966, Rodd & Boonstra 1984, but see Wolff 1985b).

Table 14: Simple linear correlation analysis of numbers captured (N_C) and number of residents (N_R) versus MMDM and A_t. Correlation coefficient, r, with coefficient of determination (r^2). All correlations significant P<0,01, $r_{(2,10)}$=0,708.

	MKN		ACW	
	MMDM	A_t	MMDM	A_t
N_C	-0,75 (0,56)	-0,76 (0,58)	-0,73 (0,53)	-0,78 (0,61)
N_R	-0,71 (0,50)	-0,73 (0,53)	-0,74 (0,55)	-0,78 (0,61)

Additional estimates of N and A_t were desired in Session 6 to provide a check on the Schumacher and MMDM results. These were obtained by using assessment lines (Table 15). The A_t values calculated were nearly twice as large as those calculated by the MMDM for Session 6 (Tables 13 and 15). Community size estimates (N_A) were also nearly twice as large as the Schumacher estimates. In the MKN, N_A was 760 animals versus 438 for the Schumacher estimate while the two estimates were 335 and 210 respectively in the ACW. While these very large differences in the estimates of size and area raise some questions about what was actually sampled from where, the important fact is that the density estimates were nearly identical (Table 15, Fig. 12a). In the MKN, density was estimated at 35 a/ha using the Schumacher-MMDM method while the assessment line method estimated density at 32,9 a/ha. In the ACW, the estimates were even closer at 14,6 and 15,2 a/ha respectively. Thus the original density estimates in Session 6 in both habitats seem reasonable, even though the MKN trapping success was so high.

Table 15: Additional area of trapping (W_A[±SE), the total area sampled (A_t), the proportion of marked animals in the W_A (R_p) and the rodent community population estimate (N_A) and density (D) as calculated by the assessment line technique for the MKN and ACW landscapes of the KNP in Session 6 only.

Trap		Site	Habitat			
Site	W_A (m)	A_t (ha)	A_t (ha)	R_p	N_A	D
M1	43 [9]	12,9	23,1	0,52	760	32,9
M2	30 [7]	10,2				
A1	39 [7]	12,0	22,0	0,62	335	15,2
A2	29 [7]	10,0				

The density of the rodent communities throughout the study is shown in Fig. 12a. Density of both communities was very low during the drought sessions, never increasing above 3 a/ha. Although the differences between the densities of the two communities were never significant, rodent density in the MKN was always higher than in the ACW. After Session 4, both rodent communities significantly increased their densities to 15,7 and 10,7 a/ha and although the difference between their densities was larger, it was still not significant. However, by Session 6, the MKN rodent density which had continued to significantly increase, was significantly larger than the ACW community, which statistically speaking, had not increased beyond the Session 5 level (Fig. 12a).

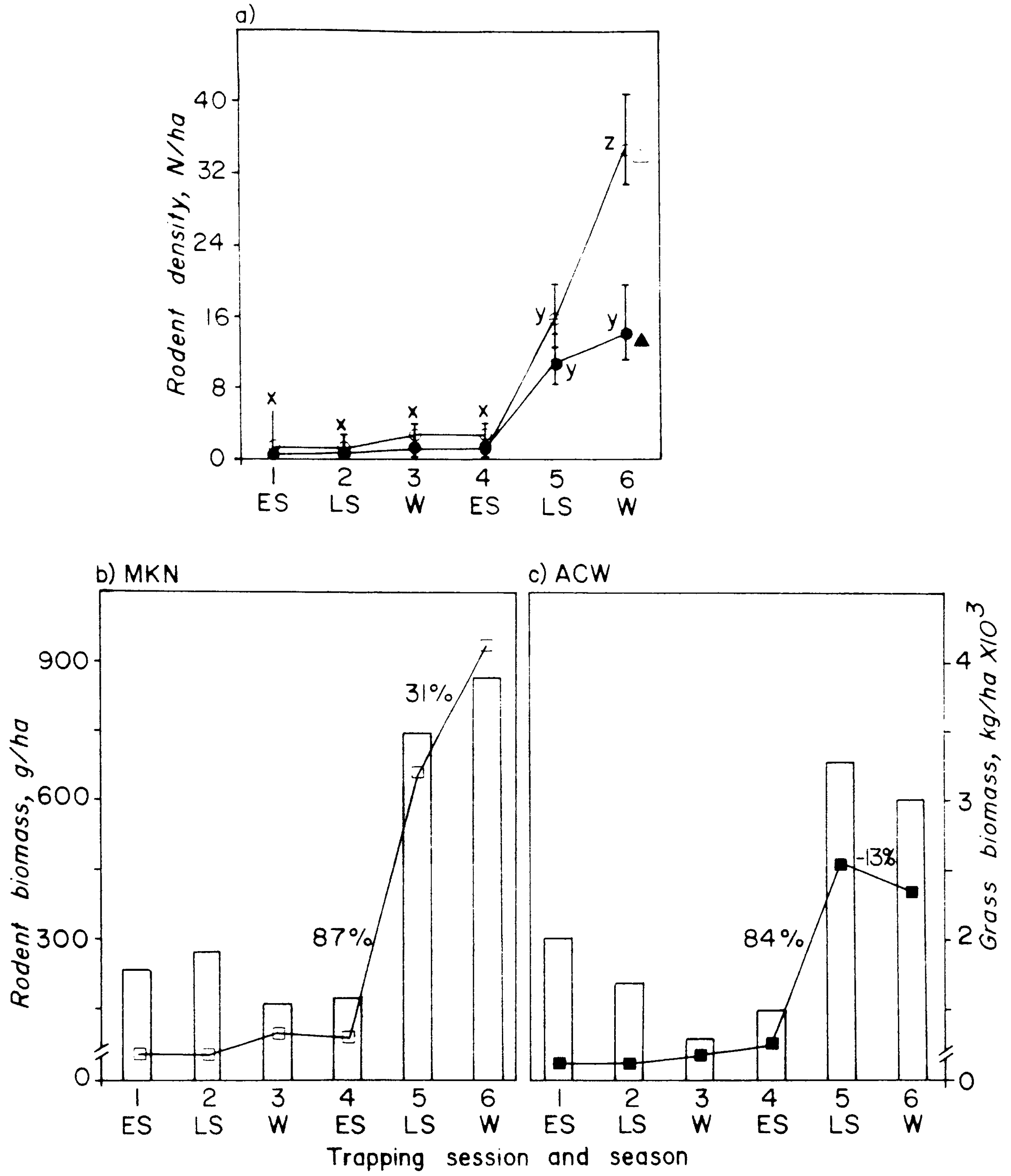

Figure 12: Rodent density with 95% c.l. (a) and rodent biomass (b, c line graph) overlaying the grass biomass (b, c bar graph) in the MKN (b) and ACW (c) landscapes of the KNP. Percentage increase in rodent biomass included in b) and c). Open and closed symbols denote MKN and ACW results respectively. Shared lower case letters (x,y,z) indicate no significant difference (P<0,05) between results. ▲ and △ in a) are density estimates determined by the assessment line technique (O'Farrell *et al.* 1977).

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Figures 12b and 12c show the changes in total rodent biomass (line graph) in comparison to the grass biomass (bar graph) in each habitat. The trend in rodent biomass in the two habitats throughout the study clearly reflects the density trends (Fig. 12a). During the drought, neither habitat supported more than 100 g/ha of rodents, however, again the MKN always supported the higher rodent biomass. After the rains, rodent biomass increased greatly and at first equally with the MKN increasing by 87% and ACW by 84% (Fig. 12b and 12c). Later in the post-drought, the rodent biomass in the MKN increased a further 31% to 936 g/ha while the ACW declined by 13%, from a high of 465 g/ha to 406 g/ha, less than half the biomass of rodents being supported in the MKN.

The pattern in rodent density and biomass in each habitat closely resembled that of the grass biomass especially in the late post-drought. Grass biomass in the MKN continued to significantly increase as did the rodents. Although, the ACW grass biomass declined slightly and rodent density increased slightly, neither were significant changes while the supported rodent biomass decreased by 60 g/ha. As may be expected from Fig. 12, the trends in rodent density, biomass and grass biomass in each habitat are highly significantly and positively correlated. The correlation coefficients in the MKN were all greater than 0,93 (r^2=0,87, $P<0,001$) and all values in the ACW were greater than 0,90 (r^2=0,81, $P<0,001$).

Density of the two shrew communities was very low throughout the entire study with density never rising above 1,2 a/ha (Fig. 13). As shown in Table 11, the presence of shrews in the MKN was sporadic. They were basically absent during the drought and then invaded immediately following the rains but quickly declined again. Shrews were more consistent in the ACW but always in low density. Both shrew communities responded to the rains with increased numbers, however, it was only in the ACW that they maintained that increase. Shrew biomass reflects the same pattern as the density. It is interesting that while density and biomass of the rodents were always greater in the MKN, the ACW always supported the larger shrew community.

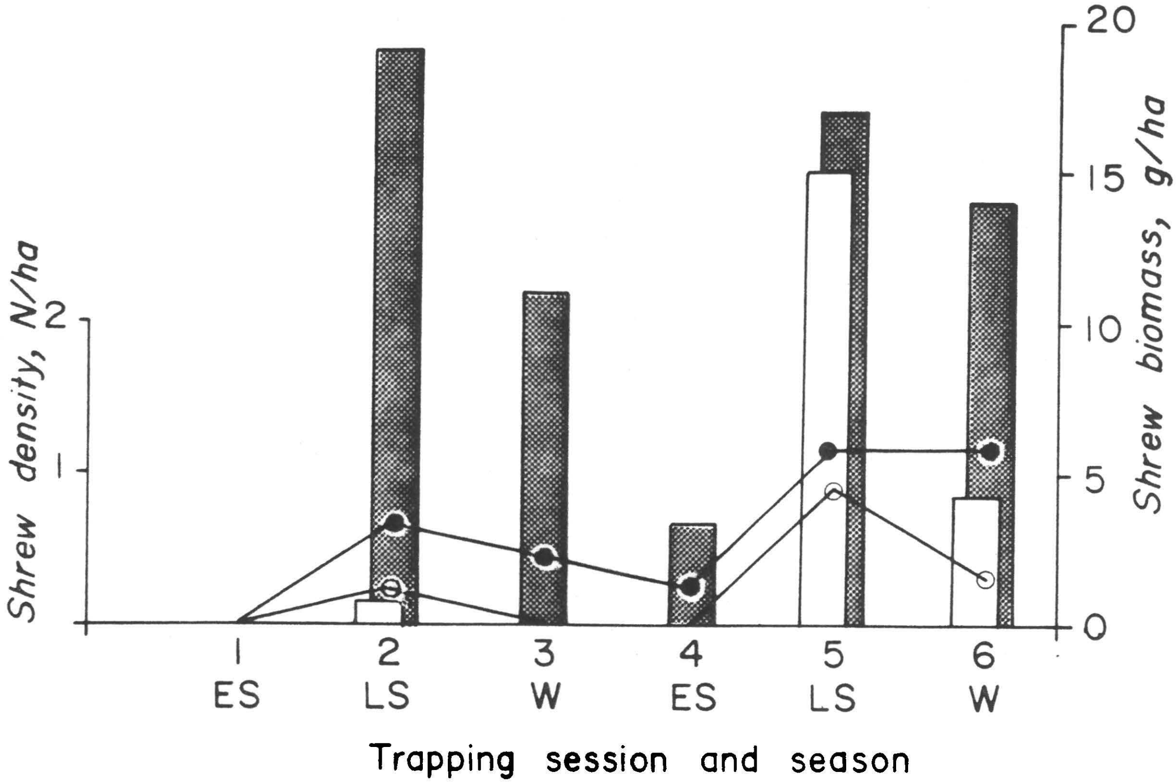

Figure 13: Shrew community density (line graphs) and biomass (bar graphs) in the MKN (open symbols/bars) and ACW (closed symbols/shaded bars) landscapes of the KNP.

The population dynamics of both the rodent and shrew communities in each habitat can be grouped into drought and post-drought periods (Fig. 12 and 13). While the shrew communities in many ways showed similar trends to the rodents, their overall numbers remained too small to realistically analyse and interpret. Therefore, growth rates and estimates of maximum stable densities were made for the rodent community only. Throughout the study's year of drought, density in the MKN only ranged from 1,4 to 2,9 a/ha which gave an observed rate of increase ($\bar{r}$) of 0,234 per session interval (or approximately 90 days) (Table 16). The situation was similar in the ACW with a density range of 0,9 to 1,6 a/ha and a $\bar{r}$ of 0,188 per session interval. During the three months following Session 4, the rates of density increase in the MKN and the ACW were very high at 2,40 and 1,90 respectively. The r values for the pre-Session 6 interval were very different as the final density levels indicate. In the MKN, although a significant increase was recorded, the rate of increase was only one third that of the Session 4 to 5 increase (0,802, Table 16). In the ACW, $\bar{r}$ was reduced to one sixth of the Session 5 rate, that is 0,310, and this was not sufficient for a significant increase in density.

Table 16: The observed exponential rates of population increase ($\bar{r}$) and the minimum - maximum range in density (D) of the rodent communities of the MKN and ACW landscapes of the KNP in drought (Sessions 1-4) and post-drought periods (Sessions 4-5 & 5-6).

	Drought		Post - Drought			
	Sessions 1-4 (12 mons.)		Sessions 4-5 (3 mons.)		Sessions 5-6 (3 mons.)	
	D (a/ha)	$\bar{r}$	D (a/ha)	$\bar{r}$	D (a/ha)	$\bar{r}$
MKN	1,4 - 2,9	0,234	1,4 - 15,7	2,40	15,7 - 35,0	0,802
ACW	0,9 - 1,6	0,188	1,6 - 10,7	1,90	10,7 - 14,6	0,310

The estimated rodent maximum stable density or carrying capacity (K) of each habitat in the drought and post-drought conditions are presented in Table 17. During the drought, the carrying capacity of the MKN was estimated as 1,7 a/ha, which was slightly less than the 2,4 a/ha theoretically present (before jackal depredations) in the final drought session, however, these two values are not significantly different. The rodent biomass being supported in the MKN at that time was 86 g/ha (Fig. 13). Estimated carrying capacity of the ACW was very similar to the final drought density estimate at 1,8 a/ha (Table 17), while rodent biomass at the time was 75 g/ha (Fig. 13). Carrying capacities of the habitats in the post-drought were quite different. Based on the population growth curve from Session 4 to 6, the MKN K was estimated at 37,7 a/ha with a potential range in K of 33,7 to 44,7 a/ha. Final rodent density at the time was 35,0 a/ha, thus it appears that the MKN community was rapidly approaching the habitat's apparent post-drought carrying capacity. Nevertheless, the final percentage increase in biomass was still a large 31% and it seems quite likely that rodent biomass would increase beyond 1,0 kg/ha. The ACW, on the other hand, showed a final density of 14,6 a/ha which was virtually at the habitat's estimated K of 14,9 a/ha. However, ACW rodent biomass at this time actually decreased, despite a slight increase in density, which suggests that approximately 400 g/ha may have been the maximum supportable rodent biomass in the ACW under the environmental conditions at that time.

Table 17: Final rodent density (D) and estimated rodent carrying capacity (K [95% c.l.]) for the MKN and ACW landscapes of the KNP in drought and post-drought conditions.

	Drought Sessions 1 - 4		Post - Drought Sessions 4 - 6	
	D (a/ha)	K (a/ha)	D (a/ha)	K(a/ha)
MKN	2,4	1,7 [0,4-3,8]	35,0	37,7 [33,7-44,7]
ACW	1,6	1,8 [0,9-2,9]	14,6	14,9 [11,5-20,6]

DISCUSSION

It was the purpose of this chapter to outline the rodent and shrew community dynamics. The brief account of species' responses (Table 11) established that changes in community composition and trends in species responses throughout the study were qualitatively similar and in the case of the two dominant species quantitatively similar as well. However, the methods for sampling the communities were not entirely appropriate for both the rodents and shrews.

First, the use of live-traps and a grain-based bait is readily acceptable as a sampling method for granivorous rodents, however, it is questionable for capturing insectivorous shrews (Brown 1967, Briese & Smith 1974, Maddock 1986 but see Beer 1964). The use of pitfall traps and/or a meat-based bait was considered not feasible because sufficient pitfall traps were not available and the extreme hardness of the ground, after a year of drought, made the placement of the traps impossible. Also, animals captured in them could not be protected from either weather or predators. With these restraints, it was accepted then that shrews were probably going to be under-sampled. Because of this, density was determined as simply as possible, using just number of individuals captured / minimum area of the trap lines. The fact that this trapping bias would exist in both habitat types meant that the relative relationships between the shrew communities were probably accurate.

Secondly, while the use of live-traps was acceptable for the rodents as a means of capture, the limited number of traps, when trapping success was high, may have caused an under-sampling of small mammal community and this must be kept in mind when interpreting the results.

The overall small mammal community composition in both habitats was very similar. As the two landscapes were adjacent, shared some similar features and had no large geograhpical barriers to inhibit small mammal movement (Chapters 2 and 3), the similarity in the small mammal faunas is not surprising. The conspicuous presence or absence of particular species in one habitat and not the other can be regarded therefore, as an active response to some specific habitat feature/s.

The absence of _Aethomys chrysophilus_ from the MKN trapping sites is a case in point. The species distribution map in Pienaar _et al._ (1980) shows their presence there, however, Kern (1981) did not record the species in his MKN trapping sites either. Both Rautenbach (1982) and Smithers (1983) claim _A. chrysophilus_ is generally ubiquitous, occurring in dense grasslands, scrub and woodland savannas. Pienaar _et al._ (1980) says the species is associated with the woodland areas in the KNP. The consistent absence of _A. chrysophilus_ in the MKN found by Kern (1981) and myself suggests that a specific habitat feature is limiting their distribution, such as the lack of developed woodland areas in the MKN habitat. However, a more detailed study of their habitat requirements is needed before more firm statements about their presence/absence can be made.

The absence of _Aethomys namaquensis_ from the ACW trapping areas appears to be a similar situation, however, it is known that this species has a strong association with pronounced rocky areas (Smithers 1983), a microhabitat which was not represented in the ACW trapping sites. The A. namaquensis present in the MKN were trapped only in the rocky ridge of the M1 trapping area (see Fig. 7). Trapping elsewhere in the ACW in the vicinity of a rocky hill, revealed their presence in the habitat. Thus their presence or the lack of it in the ACW, was associated not with the particular habitat type but rather with the presence of a particular habitat feature, namely rocks.

Also interesting, is the similar decline of Steatomys pratensis in both habitats as the drought progressed, with no re-occurrence of the species following the rains. Information on the habitat preferences of S. pratensis is sparse and conflicting, which Pienaar et al. (1980) suggests is due to the difficulty in trapping this species. Habitat preferences range from woodland to grassland areas, from sparse to dense grass cover and in arid to riverine situations (Pienaar et al. 1980, De Graaf 1981, Rautenbach 1982, Smithers 1983). The one point of concurrence is that they occur on sandy soils, however, I recorded greater numbers on the dense basaltic clays of the MKN than on the sandy soils of the ACW. Reasons for the species disappearance as the drought progressed and non-reappearance after the rains remain a mystery.

Despite the fairly high similarity between the two small mammal communities throughout the study, the ACW almost invariably had greater species richness and/or diversity than the MKN. Numerous authors, reporting on many different kinds of animals have found that species diversity increases with increasing habitat complexity and microhabitat availability (MacArthur, Recher & Cody 1966, Pianka 1967, Recher 1969, McCloskey 1972, Brown, J.H. 1973, Whitford 1976, Hafner 1977). It was established in Chapter 3 that the ACW was by far the more diverse habitat, thus my results fit well with this theory.

Species diversity of both habitats changed with time and climatic conditions. The ACW species diversity was rather erratic during the drought but stabilised at a high level after the rains while the MKN diversity was higher during the drought and declined quite dramatically after the rains. Whitford (1976) found rodent species diversity in the North American deserts greatly increased after drought breaking rains, due to increased species richness. My results show the opposite but the increased primary productivity following the rains in Whitford's study actually increased habitat heterogeneity, whereas in the MKN, it decreased habitat heterogeneity while it remained the same in the ACW (Chapter 3) which would explain the contradiction. Thus, the MKN small mammal species diversity was higher when the habitat or at least grass biomass diversity was higher. Unlike Whitford's results, however, the decrease in MKN species diversity was not due to reduced species richness but to the rapid expansion and numerical dominance of one species and the declining number of individuals of the other species. Price & Waser (1984) show not only that a greater number of microhabitats leads to increased number of species,but also that the relative abundance of each species correlates with the relative abundance of their preferred microhabitat. Additionally, Abramsky (1978) showed that species diversity actually decreased as primary production increased. Thus while the MKN offered a variety of low productivity microhabitats during the drought, a number of species were present but in relatively low numbers. Following the rains and the increased primary production, one large microhabitat, that of the dense grassland, obscurred all others (see Chapter 6, Table 27). The species compostion and diversity in the MKN seems to reflect this quite well.

In the ACW, species diversity and richness were always high but during the drought tended to be erratic. This was because small changes in the numbers of each species in a low density situation, have a large effect on the diversity index. After the rains, diversity stabilised at a high level. Productivity increased following the rains, which allowed the increased densities, however, the inherent patchiness of the habitat assured the continued availability of a variety of microhabitats.

The differences in the shrew communities of the two habitats are not as easily explained, however, I am inclined to think that food rather than microhabitat availability may be more important. Incidental observations during live-trapping indicated that the diversity and abundance of invertebrate fauna were far greater in

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the ACW than the MKN. Although this is only conjecture, it is possible that shrews were not continually present in the MKN during the drought due to a depauperate invertebrate fauna. The shrew species which was present in the MKN during the drought was Crocidura bicolor, the smallest of all the shrew species. Following the rains, it is likely that the invertebrate fauna, both the adult and larval stages, increased (Churchfield 1982), thus allowing a period of increased shrew presence in the MKN.

The methods used and compromises made in the live trapping also affected the density estimations. Most prominent was the 94% trapping success rate in the MKN Session 6. As stated earlier, Flowerdew & Gurnell (1982) suggest that a trapping success rate greater than 70% does not adequately sample the small mammal community while Andersson (1976) claimed that a trapping success rate of 30% caused a 20% underestimation of N_E. The inaccuracies in N_E would probably originate from violations of the assumption of equal catchability. Eberhardt (1969) classifies violations of equal catchability as arising from three sources:

1. An inherent behavioral avoidance (i.e. animals never captured).
2. Learned behavioral responses (i.e. animals becoming either trap-habituated or trap-shy).
3. The relative opportunity of capture for each animal (i.e. an animal must have an unoccupied trap within its home range to be captured).

The 94% trapping success rate in the MKN sixth session undoubtably reduced the opportunity of capture for each animal. This not only might have affected the estimate of N_E but also the determinations of MMDM as the farther an animal moved through the night, the chance of it finding an open trap would not increase. The obvious solution would have been to increase the number of traps per station, however, as no more traps were available, the use of a second density estimation method was used to provide a check on the Schumacher estimate. Although the assessment line technique also relies on a sufficient number of traps being available for capture, the repositioning of the traps should at least initially increase the opportunity of capture by reducing the bias caused by the previously learned trap positions.

The remarkable closeness in the density estimations in the sixth session (35,0 and 32,9 a/ha in MKN and 14,6 and 15,2 a/ha in ACW) suggests that the accuracy of the original Schumacher estimates was reasonable at both the high 94% trapping success rate in the MKN and at the lower 49% rate in the ACW. However, the fact that the assessment line results for N_A and A_t were nearly twice as large as those obtained by the original methods alerts one to the fact that the populations and area are not being measured on the same scale. The use of MMDM method on parallel census lines is probably less reliable than the assessment lines to estimate A_t because the movements of small mammals are not necessarily confined to the unidirectional plane of the traplines. The alignment of the assessment lines at 45^o angles to the census lines allows a more 360^o approach to the assessment of movement. A continual check on A_t as estimated by MMDM by the assessment lines would have been preferable throughout the study, however, Smith et al. (1971) acknowledge that this method does not work well if density of animals is low and so assessment lines would not have been appropriate during the drought sessions.

The accuracies of the MKN Session 3 and 4 densities were questioned because the Schumacher check on equal catchability in Session 3 showed that the assumption had been violated while in Session 4 the density estimate was well below the number of animals actually marked. The reasons for both these problems probably resulted from the jackal depredation of the traps. The jackals became proficient in opening traps only during the last few days of Session 3 and although the jackals killed only 6 animals, these individuals were not available for recapture, which altered the ratio of marked to unmarked captured in the remaining days. To the mark-recapture model, which assumes that the population is closed or that no animal enters (born or immigration) or leaves (death or emigration) over the trapping period, this non-recapture of marked animals would appear to be unequal catchability (in this case, a learned behavioural avoidance of the traps after first capture (Eberhardt 1969)). Thus the check on equal catchability was probably reflecting the violation of the closed population assumption rather than equal catchability. I feel that the density estimate in MKN Session 3 is still reasonably accurate as it is in close agreement with the number of animals actually caught and, because the deaths occurred near the end of the session, the MMDM and A_t results were largely unaffected.

This is in clear contrast to the situation in MKN Session 4. The closed population assumption was violated and the Schumacher N_E was a gross underestimate. Equal catchability apparently was not violated probably because the session was halted while the trap protectors were made and then resumed, thereby allowing a reasonable number of recaptures after the depredations had been stopped, to satisfy the equal catchability check and for reasonable A_t estimates. Because of the obvious violation of the closed population assumption, the Jolly-Seber stochastic model was then used, however, due to its sensitivity to low capture/recapture samples (Menkens & Anderson 1986), the confidence limits around its estimates were ridiculously large. Due to the lack of reliability in the Jolly-Seber estimate, I decided to simply use the number of marked individuals as the theoretical estimate of population size (i.e. before jackal interference) while the number of marked animals minus the number killed was the real estimate for the calculation of the population rate of increase between Sessions 4 and 5. However, it must be recognised that these estimates probably represent minimum densities.

The density of the small mammal communities changed greatly during the study. However, the changes were not always associated with the breeding season as would be expected. There was no significant difference in the density both within and between the two habitats during the drought despite the passage of an entire year which encompassed an active breeding season. Density during the drought never exceeded 3 a/ha in either habitat. The biomass of rodents present also did not change very much during the drought, staying below 100 g/ha in both habitats. It has often been shown that habitat quality influences the small mammal community (Goertz 1964, Grant & Morris 1971, Birney _et al._ 1976, Grant _et al._ 1977, The lack of community growth during the drought could have been caused by any number or combination of factors working on the community as a whole or on particular species. Both food and cover could have been limiting as grass cover and seed production by the plants were very low throughout the drought. Low food availability could have affected population growth by causing poor nutritional status and poor breeding success of the adult population and in addition, poor survival of any newly weaned young. The low cover would have increased the risk of predation.

Following onset of the rains, rodent density and biomass in both habitats increased markedly and although the difference between the densities was much greater, this was still not significant. The observed rates of density increase (2,40 and 1,90) and the percentage increase in biomass (87% and 84%) in both communities were very high. The MKN community rate of increase, using the reduced population estimate of 44 animals and density of 1,4 a/ha, was higher than that of the ACW. If the higher population estimate, that of 75 animals (number marked), the density estimate is 2,4 a/ha. Interestingly, by using this density value in the calculation of $\bar{r}$ would have yielded a 1,88 rate of increase, a figure very close to the rate observed in the ACW. This suggests that a rate of increase around 1,90 may be the genetic potential (r_m) for both communities. Assuming this is so, then the MKN's $\bar{r}$ being greater than the r_m indicates that immigration as well as reproduction was increasing the population size. The rapidly reduced density in the MKN may have created just such an opportunity for a higher level of immigration.

As mentioned before, $\bar{r}$ is the observed rate of population increase as the population is influenced by environmental factors while r_m is the population's genetic potential for increase in a totally unlimited environment, that is, neither social nor resource limitations are present. During Session 4, rodent density was low in both habitats (<3 a/ha) with breeding activity just starting and primary production of the grass layer showing a slight spring increase. Following the rains, primary production flourished in both habitats thus providing an abundance of food and cover. Under these conditions of low density and abundant food and cover, by the r_m definition, it is reasonable to expect that the $\bar{r}$ values reported for both communities in Session 5 may have been equal to or in the case of the MKN, probably in excess of the r_m values. If this is so then, the $\bar{r}$ values obtained during the drought show that both communities were under severe limitations. At such low drought densities it is more likely to have been environmental rather than social limitations, however, the question of whether food or cover was the dominant limiting factor remains (see Chapters 6 & 7).

Rodent densities by Session 6 were, for the first time, largely and significantly different. The growth patterns were also quite different with the MKN maintaining a significant level of increase while the ACW population did not. Examination of the $\bar{r}$ values shows that while the MKN was still significantly increasing, the actual rate of increase had fallen from 2,40 to 0,802, thus it seems that limitations of some kind were affecting population growth. However, a reduced rate of increase was expected as the breeding season had ended a month or so prior to trapping. The fact that the $\bar{r}$ values in the MKN and ACW were no longer similar, the ACW $\bar{r}$ was only a third of the MKN value, suggests that the environmental and/or social limitations in the ACW were greater than in the MKN.

The combination of rodent density, rodent biomass and grass biomass results presented in Figure 12 and the high and similar correlation coefficients reported, suggest that each habitat's rodent carrying capacity is strongly related to its grass condition. Grant et al. (1977) also showed a strong relationship between grassland vegetation biomass and small mammal biomass. The estimation of carrying capacity (K) assumes that a population is striving for a steady state at the maximum density each habitat can support (Caughley 1977). The estimates of K and its 95% confidence intervals in the drought and post-drought periods suggest that both communities were at each habitat's carrying capacity during the drought and that the ACW community, more than the MKN community, had reached maximum density by the sixth session. The predicted K for the MKN was approximately 38 a/ha thus the MKN community, although nearing K may have had a small potential for continued increase. However, confirmation of this estimate could only have been obtained if a seventh trapping session had been conducted. The fact that the K estimates agree so well with the density figures is not surprising as the estimate arises from the density data. However, the fact that the rodent biomass showed a large increase leading into the last session despite nearing the estimated density K may suggest that a social limit was being neared rather than an energetic (available food energy) limit. The decrease in rodent biomass in the ACW despite a slight density increase (although it was not a significant increase) suggests that the estimate of the ACW habitat's rodent carrying capacity is probably quite valid and that it may be an energetically determined capacity.

The lower rodent carrying capacity in the ACW could have resulted from numerous environmental and/or social limitations, which may or may not have been the same limitations experienced by both communities during the drought. Grant (1975) showed a woodland habitat to have a much lower carrying capacity of voles than a grassland hab,itat and sugested that this was not energetically limited but predator limited. The very patchiness of the ACW, which assured a variety of microhabitats, also assured the continued occurrence of some very low cover, high predator risk areas. If predators were limiting in the drought and in Session 6, why were they not equally as limiting in Session 5? Andersson & Erlinge (1975) in their review of predation on rodent populations, show that the density and thus the influence of resident predators lag behind the rodent populations because of the length of the predators' own generation time. The greatest predator influence occurs as the prey population reaches its own climax and additional generations of predators enter the system (Pearson 1966). Nomadic rodent specialists would have had a more immediate and severe impact, however, they generally require very abundant prey populations (Andersson & Erlinge 1975), which the ACW community was not, especially in contrast to the MKN community.

Food could also have become limiting as the primary productivity of the grass declined in the last session, however, that assumes that the rodents did not have sufficient secondary food items such as insects or tree seeds to supplement their diets in the ACW. Unfortunately, the status of the insect populations was not investigated but it was noted that the majority of trees had not dropped their seeds by the end of the study (Chapter 3).

Microhabitat availability is a third possible limiting factor. Feldhamer (1979) showed that high structural diversity in a habitat correlates with high small mammal diversity but low numbers while low structural diversity resulted in high numbers but low diversity. Likewise, Price & Waser (1984) showed a correlation between the relative abundance of each species with the relative abundance of its preferred microhabitat. While limited microhabitat size is a distinct possibility for the rodent communities in this study, these effects would operate primarily on the species level and only secondarily at the community level. This aspect is explored more fully in Chapter 6. Both food and predators are likely to operate in a more indiscriminant manner.

It is unlikely, however, that determination of one dominant factor which influences the carrying capacity of both habitats will be found. It is far more likely to be a multitude of factors, similar in some respects but dissimilar in others which limited the communities in each habitat and in each climatic period. Certainly what would have been most interesting is if an additional theoretical estimate of K, based on potential available energy, could have been calculated for each habitat. However, to obtain such results would have required a detailed labour-intensive study of each species' diet and metabolic requirements and each habitat's food availability. Nevertheless, the results of such a study would estimate each habitat's rodent carrying capacity based on energy potential and this compared with the actual rodent densities and biomass could provide tremendous insights into the importance of resource versus predator/social limitations in the two habitats.

CHAPTER FIVE

POPULATION DYNAMICS OF SACCOSTOMUS CAMPESTRIS, PRAOMYS COUCHA AND PRAOMYS NATALENSIS

INTRODUCTION

The previous chapter showed that the densities of small mammals, especially the rodent communities, were equally low in both habitats during the drought and responded similarly immediately after the onset of the rains. However, in the late post-drought period the density and biomass of the rodent community in the ACW were much less than in the MKN, indicating that the ACW community was being limited by some unique factor.

As the state of the small mammal community at any one time is but a sum total of the densities of each species present, the question arises whether the factors affecting the small mammal communities were influencing the communities generally, irrespective of species, or if different factors were involved in the regulation of each species. As already shown briefly in the previous chapter, the density responses of the thirteen species to the changing climatic and physical conditions were not always similar, thus individual factors regulating each species must be examined.

This is explored in more detail by comparing the densities of three of the more common species, namely Saccostomus campestris, Praomys coucha and Praomys natalensis. Based on total numbers of animals marked, the population dynamics of Tatera leucogaster could also have been analysed, however, the even distribution of captures over the study period meant that numbers remained relatively low throughout the study. This makes population analyses both difficult and unreliable due to small sample sizes. While the number of P. natalensis captured was only slightly higher (72 cf 70) the population dynamics of this species is examined for two reasons. First, the number captured in the final session, especially in the ACW, was sufficiently

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large for reasonable population estimates and second, its distribution and population responses in each habitat make an interesting comparison with *P. coucha*, a closely related sibling species (Gordon 1984).

The main purpose of this chapter is to determine what intrinsic factors may have been influencing the population dynamics of the three species, how and why. Factors such as the length of the breeding season, intensity of breeding activity, sex ratios and the population age structures all provide information as to the success and cost to each species of efforts to reproduce and increase population size. In addition, an understanding of some of these basic population parameters can lead to suggestions as to when and what other influences, extrinsic in nature, could have been important.

METHODS AND MATERIALS

Live-trapping Programme

The methods used in the live-trapping programme have already been detailed in Chapter 4. I became aware of the cryptic species relationship between *Praomys natalensis* and *P. coucha* six months after the study had started. Fortunately, *Praomys* numbers were still low. Initially, I endeavored to obtain blood samples from all *Praomys* individuals for species identification by electrophoretic analysis (see Gordon & Watson 1986). However, as the numbers of *Praomys* captured increased, logistical and financial limitations in the collecting and electrophoretic analysis of the blood samples demanded compromises. Preliminary results showed that *P. coucha* and *P. natalensis* coexisted in the ACW while only *P. coucha* occurred in the MKN (see results below). It was decided therefore, to sample all *Praomys* individuals captured in the ACW and to randomly sample individuals from the MKN. A stratified sampling scheme was followed whereby a blood sample was taken from every second new capture. In Session 6, however, this had to be amended to every third new capture because of the very large numbers of *Praomys* captured.

As described in Chapter 4, each captive was weighed and had its sex and breeding condition determined. Individuals were assigned to relative age classes based primarily on their body mass measurements, however, on occasion, pelage appearance was also used. Table 18 lists the mass/age criteria used for each species. The mass/age delineations were set based on personal experience, general southern African mammal biology references (De Graaf 1981, Rautenbach 1982, Smithers 1983) and, where available, detailed publications on the post-natal development of particular species.

Also dependent to some extent on the mass/age criteria was the determination of the number of animals of reproductive age. Both adult and sub-adult animals were considered as being of reproductive age, according to the definitions stated by De Blase & Martin (1981).

Adult :	The larger and potentially breeding members of a population.
Sub-adult:	A young of the year that may or may not be in breeding condition. It is typically smaller than an adult but otherwise is similar.
Juvenile :	An individual smaller than a sub-adult and often but not always has a pelage colouration distinct from that of the sub-adults and adults.

Population Parameters

Density of S. campestris, P. coucha and P. natalensis was estimated as described in Chapter 4. However, species specific estimates of the area of trapping effect (A_t) (MMDM method, Chapter 4) were generally impossible to calculate because insufficient numbers of each species qualified as resident animals. Therefore, to obtain density estimates the population size estimate of each species (Schumacher method, Chapter 4) was divided by the appropriate habitat A_t values presented in Table 12. It is recognised, however, that this makes the doubtful assumption that all species have similar foraging or movement patterns. Nevertheless, this was considered more realistic than naive density estimates (Wilson & Anderson 1985).

Table 18: Body mass (g) criteria used in the relative age assessment of the 13 small mammal species captured in the MKN and ACW landscapes of the KNP. Body mass ranges taken from Rautenbach (1982). Superscript numbers indicate the use of published records on post-natal development to aid estimation of mass/age relationships. [a]= mass range determined from the present study due to recent recognition of this species (see text). [b]= one female in very late pregnancy weighed 80g.

	Range	Juv.	SAd.	Ad.
Rodent species				
Aethomys chrysophilus[1]	26-125	≤35	>35<55	≥55
Aethomys namaquensis[2]	28- 88	≤20	>20<35	≥35
Graphiurus murinus	15- 32	≤ 8	> 8<15	≥15
Lemniscomys griselda	27- 89	≤25	>25<35	≥35
Mus mintutoides	3- 12	≤ 4	> 4< 6	≥ 6
Praomys coucha[a]	8- 69[b]	≤18	>18<30	≥30
Praomys natalensis[3]	21- 82	≤20	>20<35	≥35
Saccostomus campestris[4]	15-100	≤25	>25<40	≥40
Steatomys pratensis	10- 44	≤10	>10<18	≥18
Tatera leucogaster	32-114	≤28	>28<45	≥45
Shrew species				
Crocidura bicolor[5]	2- 5	≤ 1,5	>1,5<2,5	≥ 2,5
Crocidura hirta[6]	8- 24	≤10	>10<15	≥15
Elephantulus brachyrynchus	31- 55	≤20	>20<30	≥30

[1]Brooks (1972), [2]Meester & Hallett (1970), [3]Meester (1960), Baker & Meester (1977), [4]Earl (1980), [5]Watson & Watson (1986), [6]Meester (1963).

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RESULTS

Blood sample analysis of the *Praomys* individuals showed that the two *Praomys* species, *P. coucha* and *P. natalensis*, coexisted in the ACW habitat while in the MKN, only *P. coucha* occurred until the final session (Table 19). Based on the Sessions 3, 4 and 5 results in the MKN, it has been assumed that the *Praomys* individuals captured in Sessions 1 and 2 were also *P. coucha*. The sudden appearance of *P. natalensis* in the MKN Session 6 was surprising. Of the blood identified individuals, 2,3% (3/131) proved to be *P. natalensis*. Assuming the sampling method was random, this suggests that possibly another five *P. natalensis* could have been amongst the unidentified animals, which would have given a population size of about eight animals. An additional three *Praomys* were selected for blood sampling (i.e. non-random sample) because of their particularly large size. ($\bar{x}$= 50,7±2,1g, n=3, cf. mean adult mass of identified *P. coucha* of 35,8±0,6g, n=68, P<0,001, t=4,78, df=69). The blood tests showed all three to be *P. natalensis*. Therefore, if the population size was about eight animals and six were definitely identified (three randomly, three non-randomly) then there was perhaps another 2 - 5 *P. natalensis* still unidentified. Because there was probably only a very low number of *P. natalensis* unidentified in the non-blood sampled *Praomys* individuals, the data arising from all the unidentified *Praomys* were considered as belonging to *P. coucha*. It was felt that the possible inclusion of a few *P. natalensis* in the *P. coucha* population analyses would have a negligible effect on the population statistics. In contrast, the exclusion of 243 of the probable 368 *P. coucha* would represent a substantial loss of *P. coucha* information.

Because of the large size of the one *Praomys* individual (51g) captured in the ACW Session 1, this animal was considered to be *P. natalensis*. This assumption of species identification, however, is of little importance to the population statistics of either species due to the sporadic presence of the two species in the ACW drought sessions anyway.

Table 19: The number of Praomys sp. individuals marked (N_m), the percentage of the population blood sampled (%pop), and the percentage of the sample identified as P. coucha (%Pc) in the MKN and ACW Praomys populations in the KNP. ES, LS and W as before.

	MKN			ACW		
Session	N_m	%pop	%Pc	N_m	%pop	%Pc
1 (ES)	6	0	?	1	0	?
2 (LS)	19	0	?	0	0	0
3 (W)	32	88	100	2	100	50
4 (ES)	38	63	100	6	100	17
5 (LS)	174	58	100	70	100	79
6 (W)	374	35	98	158	100	73

The population growth curves of the three dominant species show similar patterns during the drought and early rain conditions. Low densities occurred during the drought followed by a substantial increase with the return of the rains (Figure 14). S. campestris and P. coucha were numerically dominant in the MKN where they existed at very similar densities (1,0 to 1,3 a/ha, Figure 14a) throughout the drought, whereas the combined density of all the other species combined was always <1,0 a/ha. A similar situation existed in the ACW, however, only S. campestris showed a consistent presence (<1,0 to 1,2 a/ha, Figure 14b) during the drought.

The mean exponential rates of density increase over the drought year were all very low (Table 20). P. coucha in the MKN maintained the highest mean rate which was 0,66 per session interval. Following the rains, all species increased density at a much higher exponential rate than before (Fig. 14, Table 20). P. coucha had the highest rate of increase in both habitats. S. campestris increased at similar rates in both habitats, however, the ACW population increase was marginally better than the MKN population. The rates of increase by both Praomys species in the ACW were extremely high, especially that of P. coucha (4,60 per 3 months). As there was only one P. coucha (male) captured in the ACW in Session 4, the population increase was undoubtably a result of immigration. However, the number of small juveniles in Session 5 suggests that reproduction may have been important in the latter part of the non-trapping interval.

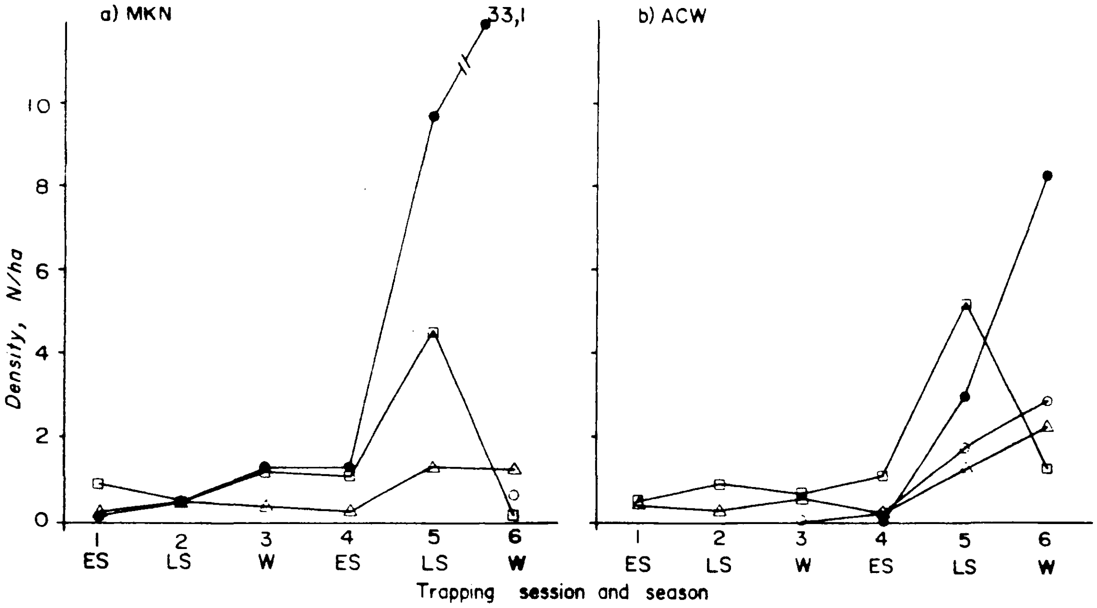

Figure 14: Density of <u>Praomys coucha</u> (●), <u>Saccostomus campestris</u> (□), <u>Praomys natalensis</u> (○) and the 'other species' combined (△) in the MKN (a) and ACW (b) landscapes of the KNP.

Differences in the densities and rates of increase in Session 6 were the most striking. <u>P. coucha</u> continued to increase, but, at a much lower rate than in Session 5. As Session 6 occurred during a non-breeding season, a decrease in the rate of increase is to be expected due to the gradual cessation of breeding activity and the reduced number of juveniles enter the populations. The rate of increase in the ACW <u>P. coucha</u> population showed a more drastic decline than the MKN population. The final densities of the two <u>P. coucha</u> populations were very different with the MKN supporting 33,1 a/ha and the ACW supporting 8,3 a/ha.

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Table 20: Observed exponential rate of density increase ($\bar{r}$) over the drought (Dr.) and post-drought (Post-Dr.) sessions for Saccostomus campestris (Sc), Praomys coucha (Pc), and Praomys natalensis (Pn) populations in the MKN and ACW landscapes of the KNP.

	MKN				ACW			
	Dr.	Post-Drought			Dr.	Post-Drought		
	1-4	4-5	5-6	4-6	1-4	4-5	5-6	4-6
Sc	0,15	1,43	-3,13	-0,85	0,21	1,57	-1,41	0,84
Pc	0,66	2,01	1,23	1,62	----	4,60	1,02	2,23
Pn	----	----	----	----	----	2,20	0,48	1,34

The rate of increase for P. natalensis had decreased well below the level of both the P. coucha populations. The final P. natalensis density in the ACW was only 3,0 a/ha, an exponential increase of only 0,48 (Fig. 14, Table 20). The decline in the rates of increase for the ACW P. coucha and P. natalensis populations between Sessions 4-5 and 5-6 represented a 77-78% decrease for both species.

The two S. campestris populations showed a strikingly similar pattern to each other but a very different pattern to all the other species. The MKN population declined from 4,6 to 0,2 a/ha and the ACW population declined from 5,6 to 1,3 a/ha just in the three months between Sessions 5 and 6. The final densities of S. campestris, P. natalensis and the 'other species' were all at higher levels in the ACW than in the MKN. Conversely, P. coucha was at a much higher density in the MKN than any other species either in the MKN, in the ACW, or even for the ACW community as a whole (Fig. 14, 12a and 13).

It was apparent in both habitats that population growth of all three species, and indeed for the 'other species' as well, was severely limited during the entire drought period. In Session 6, there was no longer any real similarity in the population responses, suggesting that the species may have been facing differentially limiting situations. Even within species, the two populations reacted differently. The rest of this chapter will explore possible reasons for the observed population limitations and differences, both between climatic periods and between habitat types.

The breeding season (Smithers 1983) for all the species encountered in the present study spans the wet summer months from approximately October / November to March / April which coincides with the early and late summer trapping sessions 1, 2, 4 and 5. During these sessions, high percentages of animals of reproductive age, that is animals in the adult and sub-adult age classes, were recorded in active breeding condition both in the drought (Sessions 1, 2 and 4) and in the post-drought conditions (Session 5) (Table 21). The populations in both habitats in the two winter sessions (3 and 6) showed either very low or no breeding activity. Thus there was a considerable and similar breeding effort made by all species in the breeding seasons of both years of the study, that is regardless of the drought or post-drought conditions.

Table 21: Percentage of the reproductive age (Sub-adult and Adult) *Saccostomus campestris* (Sc), *Praomys coucha* (Pc) and *Praomys natalensis* (Pn) populations in active breeding condition in the MKN and ACW landscapes of the KNP. The number of reproductive age animals marked in brackets. ES,LS and W as before.

	MKN			ACW		
Session	Sc	Pc	Pn	Sc	Pc	Pn
1 (ES)	82 [21]	50 [6]	-------	70 [10]	-------	100 [1]
2 (LS)	85 [20]	53 [17]	-------	60 [15]	-------	--------
3 (W)	7 [29]	5 [19]	-------	14 [14]	0 [1]	0 [1]
4 (ES)	68 [25]	52 [29]	-------	81 [32]	0 [1]	60 [5]
5 (LS)	78 [83]	66 [130]	-------	44 [97]	56 [50]	82 [11]
6 (W)	0 [3]	0 [338]	0 [5]	0 [16]	0 [68]	0 [25]

During the drought sessions (1-4), adult sex ratios for all three species were biased in favour of males (Table 22). However, not all were significantly different from the expected 1:1 ratio (Chi-square test). The MKN species showed the greatest

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number of significantly biased sex ratios during the drought. Three out of the four MKN S. campestris adult sex ratios in the drought were significant at levels less than P<0,05 while the fourth (Session 3) was only just non-significant at P=0,063 (Table 22, Fig. 15A-D). Two out of the four P. coucha adult sex ratios were also significantly different from 1:1 (Table 22, Fig. 16A-D). Despite a few of the drought session adult sex ratios being not significantly different from 1:1, the overall trend to low numbers of adult females was highly significant (Fisher's combined probabilities test, Sokal & Rohlf 1981). Both S. campestris and P. coucha in the MKN showed significant trends (P<0,001, χ^2= 29,84, df=8 and P<0,005, χ^2=23,52, df=8 respectively), however, the male-biased trend for S. campestris in the ACW was not significant (P>0,10, χ^2=11,59). In contrast to the adult situation, none of the non-adult sex ratios for any species were significantly different from 1:1. This suggests that either there was a difference in trapping success for adult females or that they were suffering high mortality.

Table 22: Adult (Ad) and non-adult (N) sex ratios (female : male) of Saccostomus campestris (Sc), Praomys coucha (Pc) and P. natalensis (Pn) populations in the MKN and ACW landscapes of the KNP. * - significant difference from expected 1:1 ratio, P<0,05, χ^2=3,841, df=1. ES, LS and W as before.

Session	Age	Sc	Pc	Pn	Sc	Pc	Pn
1 (ES)	Ad	1,0:4,0*	1,0:1,5	----	1,0:1,5	----	----
	N	2,0: 0	1,0: 0	----	1,0:0,8	----	----
2 (LS)	Ad	1,0:3,0*	1,0:3,0	----	1,0:2,5	----	----
	N	1,0:5,0	1,0:0,4	----	1,0:1,7	----	----
3 (W)	Ad	1,0:2,6	0 :7,0*	----	1,0:2,0	----	----
	N	1,0:0,8	1,0:0,8	----	1,0:0,4	----	----
4 (ES)	Ad	1,0:4,3*	1,0:3,3*	----	1,0:2,2*	----	0 :3,0
	N	1,0:0,7	1,0:0,5	----	1,0:1,0	----	2,0: 0
5 (LS)	Ad	1,0:2,2*	1,0:1,0	----	1,0:1,5	1,0:5,8*	0 :6,0*
	N	1,0:1,5	1,0:1,4	----	1,0:1,3	1,0:0,5	1,0:0,8
6 (W)	Ad	1,0:2,0	1,0:1,1	1,0:2,0	1,0:1,2	1,0:1,2	0 :9,0*
	N	0 : 0	1,0:1,1	1,0:0,5	1,0:2,0	1,0:1,1	1,0:1,3

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Adult sex ratios in the post-drought sessions (5 & 6) varied between species and habitat. Adult sex ratios in the S. campestris populations of the MKN continued to show a strong male bias throughout the post-drought, however, only the Session 5 ratio was significant. The significantly male-biased sex ratio is rather surprising as much larger numbers of adult S. campestris females were caught in Session 5 than in either the drought sessions or later in Session 6 (Fig. 15A-F). In the ACW, the adult sex ratios of the post-drought S. campestris populations were approaching 1:1 (Table 22, Fig. 15K-L). In the MKN post-drought P. coucha population, the sexes were equally represented (Table 22, Fig. 16E-F). The ACW population, however, still showed a strongly male biased sex ratio in Session 5 which equalised only in Session 6 (Table 22, Fig. 16K-L). No adult female P. natalensis were ever caught in the ACW in the drought or post-drought periods, however, one was trapped in the MKN Session 6 (Fig. 17f).

The non-adult sex ratios were again all approximately 1:1 (Table 22). The closer approximation of a 1:1 adult sex ratio and/or the increased number of females trapped in the post-drought period (except P. natalensis) suggests that the females were not inherently avoiding the traps in the drought and that mortality may have been high instead.

How successful the breeding efforts were can be seen in the age structure diagrams (Fig. 15, 16 and 17). The number of non-adults actually entering the populations during the drought varied between species and habitat. S. campestris, in general, had a lower number and proportion of non-adults entering the population in the MKN than in the ACW (Fig. 15A-D, G-J). However, even in the ACW population, the proportion of non-adults in the population was very low. Following the rains, the proportion of non-adults actually decreased (Fig. 15E-F, K-L), suggesting that breeding success on my traplines had not improved. However, apparently breeding success had improved somewhere because S. campestris numbers had greatly increased.

In contrast, P. natalensis in the ACW post-drought had a high proportion of non-adults, with the adult to non-adult ratio being 1:1,5 in Session 5 and 1:3,7 in Session 6 (Fig. 17K-L).

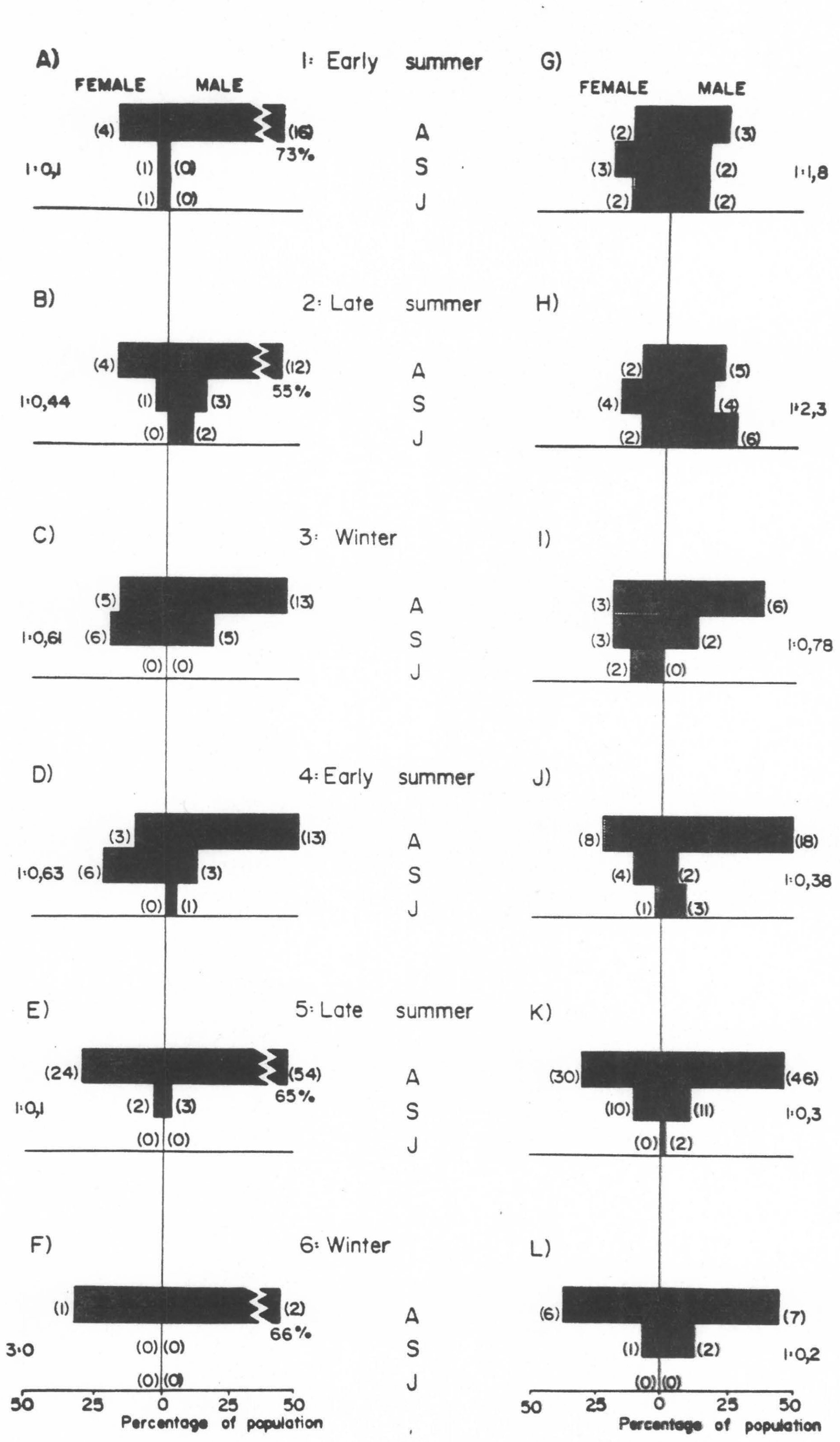

Figure 15: Age structure diagrams of the Saccostomus campestris populations in the MKN (A-F) and ACW (G-L) landscapes of the KNP. The adult:non-adult ratios are given on the outer side of each diagram. The number captured in each age class is given in ().

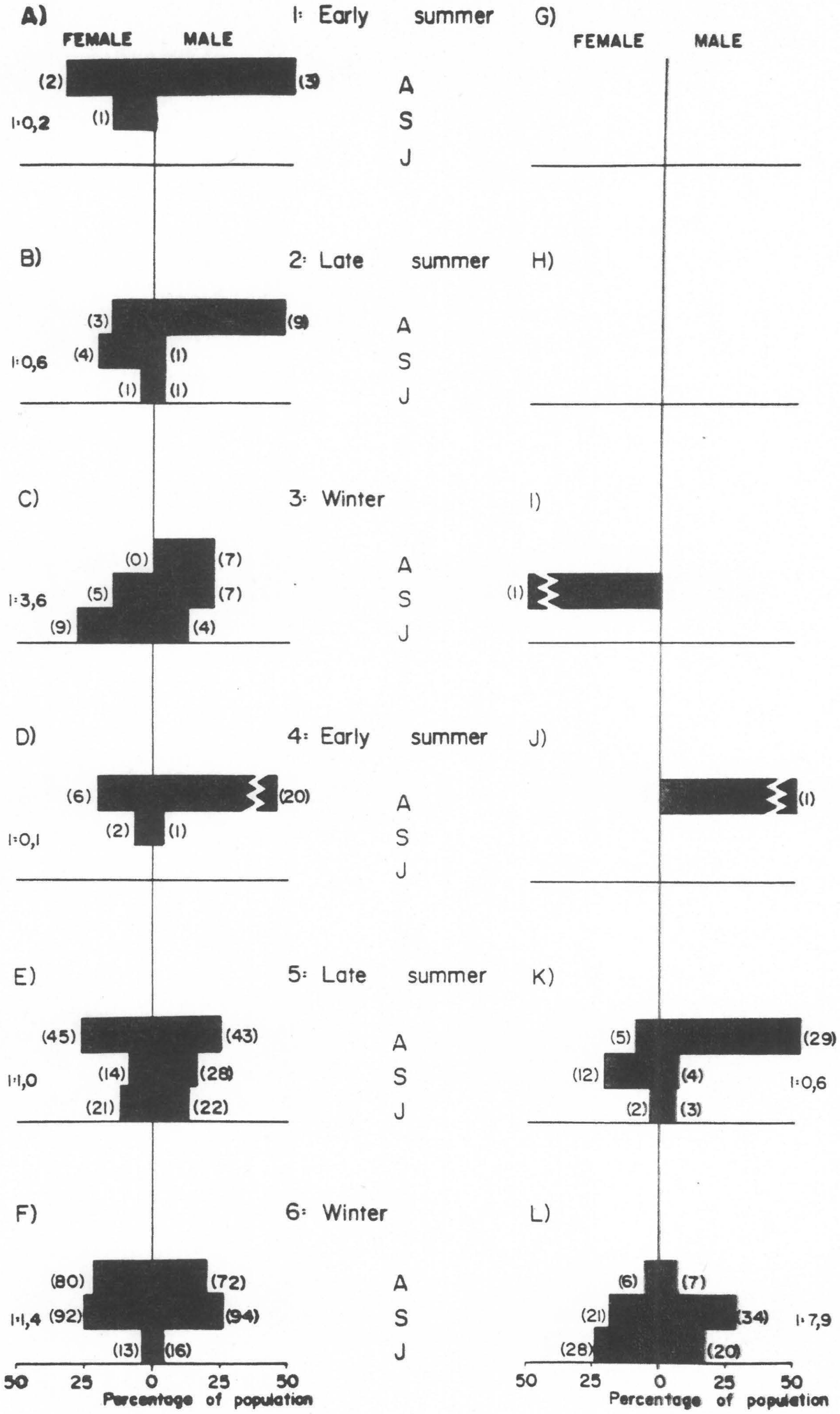

Figure 16: Age structure diagrams of the *Praomys coucha* populations in the MKN (A-F) and ACW (G-L) landscapes of the KNP. The adult:non-adult ratios are given on the outer edge of each diagram. The number captured in each age class is given in ().

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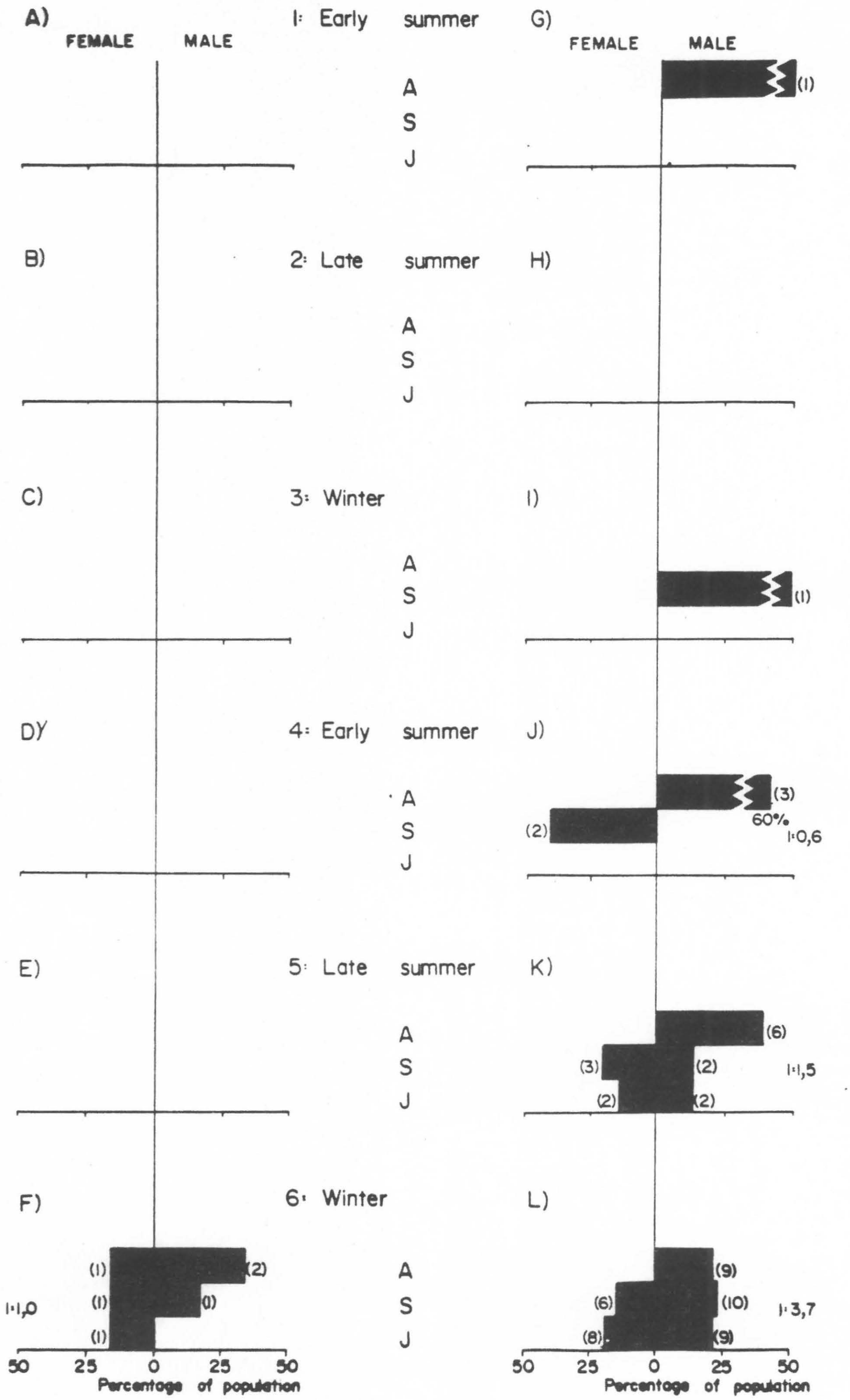

Figure 17: Age structure diagrams of the Praomys natalensis populations in the MKN (A-F) and ACW (G-L) landscapes of the KNP. The adult:non-adult ratios are given on the outer side of each diagram. The number captured in each age class is given in ().

P. coucha also tended to have low numbers of non-adults in the populations during the drought, except in the Session 3 winter season (Fig. 16A-D). This apparent breeding success may have been possible due to the massive rainstorm and temporary improvement in environmental conditions which occurred in the previous March (see Chapter 2). In the post-drought sessions, P. coucha had large numbers of non-adults entering the MKN population and the adult to non-adult ratios were close to 1:1 (Fig. 16E-F). P. coucha in the ACW showed a rather low proportion of non-adults in Session 5 but by Session 6, the opposite was true (Fig. 16K-L).

The age structure diagram for P. coucha in the ACW sixth session shows that large numbers of non-adults were still entering the population, however, comparison of the mass records of individuals captured in sequential sessions and who were non-adults at first capture suggests that the age structure diagram may have been inaccurate in its representation. During the drought, the average mass gain over a three month non-trapping interval by non-adult P. coucha in both habitats was about 21 g (Table 23). In the rain period, between Sessions 5 and 6, mass increase by the MKN non-adults was approximately 12 g per three months. Although this was less than during the drought, a 12 g increase was still sufficient for all of the animals to be classified the following session in the next higher age class. Unfortunately, the number of animals recaptured in succeeding sessions in the ACW was fairly low, however, without exception the mass gain was less than 2,5 g, with a mean of only 2,0 g per three month interval. None of the non-adults recaptured could be classified into a higher age class according to the mass/age methods used, despite a three month gain in chronological age.

Similar mass gain results for non-adult S. campestris were found in the drought, where mean mass gain by five non-adults was 26 g per three months. Unfortunately, no data was available for S. campestris in the post-drought period.

Table 23: Mean mass ($\bar{x}$) and mean mass increase ($\bar{x}$ inc., ±SE) by non-adult Praomys coucha recaptured in sequential sessions under drought and post-drought conditions in the MKN and ACW landscapes of the KNP.

	Age Class	Drought			Post-Drought		
		$\bar{x}$(g)	[n]	$\bar{x}$ inc.(g)	$\bar{x}$(g)	[n]	$\bar{x}$ inc.(g)
MKN							
	Sub-Adult	25,1	[3]	19,0	22,6	[19]	9,4
	Juvenile	16,1	[4]	22,6	16,3	[18]	14,6
	Non-Adults	19,9	[7]	21,1±2,4	19,0	[37]	11,9±0,7
ACW							
	Sub-Adult	25,3	[1]	20,9	21,8	[2]	2,6
	Juvenile	----	---	----	14,8	[3]	1,6
	Non-Adults	25,3	[1]	20,9	17,6	[5]	2,0±0,3

DISCUSSION

The population responses of Saccostomus campestris, Praomys coucha and Praomys natalensis were generally similar throughout the drought and early post-drought periods. In both habitats, densities of S. campestris and P. coucha were low with an initial high increase following the return of the rains. Although the situation for P. natalensis in the MKN was different, the ACW population responded in the same fashion as the other two species. Differences in the rates of response both between species (intra-habitat comparison) and within species (inter-habitat comparison) were evident in the early and late post-drought periods.

Analyses of breeding activity, sex ratio, and age structure for the three species during the drought showed strong similarity in many respects. Although during the drought, only S. campestris populations could be compared between habitats and only S. campestris and P. coucha could be compared within the MKN, all three populations showed common features. Despite evidence of highly active breeding populations, population growth remained stunted. Low numbers of both adult females and non-adults were recorded and while in general the adult populations showed male-biased sex ratios, the non-adult populations showed equal numbers of males and females. These results suggest three things. First, that breeding success was very low and secondly, that this may have been due to selective high mortality of the adult females, hence their low numbers. Thirdly, if mortality of the breeding females was high, this would have its greatest effect on the survival of the dependent nestlings. Such a sex-indiscriminant mortality of the young would explain the low numbers but 1:1 sex ratio of non-adults entering the populations.

The increased energetic demands of reproduction, especially lactation, on the female is well known and numerous authors have recorded poor body condition and low fat reserves of female rodents in the breeding season (Caldwell & Connell 1968, Evans 1973, Field 1975, Cole & Batzli 1979, Goudie & Vessey 1986). Fairbairn (1977) found that the decline in numbers of female Peromyscus maniculatus was due to high mortality of the early breeding females. In addition, Desy & Thompson (1983), when comparing populations on a food-supplemented grid versus a control grid, found a significantly greater number of females on their food-supplemented grid during the spring and summer seasons only, when breeding was at its highest intensity. Ostfeld, Lidicker & Heske (1985) found that female rather than male voles showed the greatest dependency on food and cover. In their study, only female survival varied with seasonal variations in resource availability. In the present study, satisfying the increased nutritional demands required by breeding may have been quite difficult and costly for all females, regardless of species because of the poor environmental conditions during the drought. If food supplies were low as hypothesised (Chapters 3 & 7), the greater energetic needs of the females in breeding condition may have required longer foraging hours. This could have substantially reduced females fitness and in the poor cover conditions increased the risk of predation, both of which would lead to increased female mortality.

This is further supported by the thought that if such demands and constraints did exist for the breeding females then the probability of trapping should have been higher for them than for the rest of the population because the longer foraging efforts would have increased their exposure to trapping. Thus, the trends toward male-biased sex ratios in the adults may represent very strong evidence for high female mortality. Of course, the possibility of inherent trap-shyness by reproducing females may also account for their low numbers. Trappability of animals has been shown to vary with changes in reproductive condition (Smith, Gardner, Gentry, Kaufman & O'Farrell 1975 and references therein). However, while this is a possible explanation here, the equal adult sex-ratios in the breeding season of the post-drought year does not support the idea and I feel that high mortality may have been a very real situation for the breeding females.

During the hard times of the drought, one might expect the food hoarding tendencies of S. campestris (Earl 1980, Smithers 1983, pers. obs.) to allow better survival of this species over the non-hoarding species such as P. coucha. Having a stored food supply would allow many individuals to avoid foraging during particular high risk times. This should allow increased survival of all members of the species. While this may be one reason why S. campestris was one of the dominant species during the drought, it did not seem to have particularly helped the females, especially in the MKN where their numbers were as low as those for P. coucha females. The trend to low numbers of adult females was present in the ACW S. campestris population as well, however, because the small sample sizes generally reduced the power of the statistical analyses it is difficult to interpret these results as being evidence for lower female mortality in the ACW.

Myers, Bailey & Dudzinski (1976) and Caughley, Grigg & Smith (1985) reported that high mortality caused by starvation was one of the major effects of drought on kangaroo populations. The effect of the inadequate food supply on female kangaroos was early cessation of lactation and then starvation of the dependent young. In addition, Richardson, Godwin, Wilkes & Cannon (1964) showed that rats receiving up to 5% dietary protein could not support any reproductive effort, however, 10% protein supported ovulation, sperm production, fertilization and gestation but was not sufficient for lactation. Only when dietary protein reached 17 - 20% could lactation be successfully maintained. Thus, if protein availability was low in the drought, the appearances of reproduction and early signs of lactation are not in contradiction to high nestling mortality. In the present study then, poor female condition and/or high female mortality due to excessively poor condition or increased exposure to predation would have a similar sex-indiscriminant mortality effect on any embryos or dependent nestlings.

An additional explanation for the low numbers of non-adults recorded during the drought is their survival once independent of the mother. They, too, would have had to cope with the same low food, poor cover conditions. In addition, the disadvantages of dispersing in a unfamiliar environment with unknown food sources is well known. Spencer & Cameron (1983) showed that subordinate and dispersing animals were forced into non-preferred habitats while Tardif & Gray (1978) showed that the feeding diversity of immigrant animals was greater than that of resident animals until they were familiar with their surroundings (but see M'Closkey 1985). Also, Metzgar (1967) showed transient mice were more likely to be taken by owls than resident animals due to a lack of familiarity with the environment. While survival of the newly independent young could also have been poor, the non-adult mass gains suggest that if and once established, starvation may not have been a major cause of non-adult mortality.

In the early rain period, patterns in density and breeding activity were again similar. All densities increased markedly and, as discussed in Chapter 4, may be a close representation of each species's intrinsic rate of increase. Most of the sex ratios were close to 1:1 and the numbers of females and non-adults trapped had increased, suggesting that female and non-adult mortality had decreased. Although the population sizes of S. campestris populations had increased, the MKN population still showed a male biased sex ratio as well as lower numbers of non-adults, which suggests that the breeding succes may still have been low for this population. Breeding success in the ACW population appeared to be only slightly better. Continued low breeding success may have been one of the reasons for the species dramatic decline in the following three months.

Both the P. coucha populations showed extremely high rates of increase. The 2,01 rate recorded in the MKN is high but given the reproductive capabilities of the Praomys (Mastomys) species complex (Gordon 1984), it is not surprising. Caughley & Krebs (1983, Fig. 6), in their examination of intrinsic versus extrinsic population regulation for a wide spectrum of mammal sizes, show the intrinsic rate of increase for P. natalensis as about 1,70, the highest for all species depicted. The 4,60 increase rate in the ACW P. coucha population is, therefore, too high to be accepted as the species genetic potential for increase. Considering that the population in the previous session had consisted of one male individual, the predominance of adult males and the still low numbers of non-adults strongly suggests that immigration accounted for a large proportion of the population increase. Sub-adult animals, more often the male sub-adults, have often been cited as the bulk of the dispersing force in an expanding population (Fairbairn 1977, Rodd & Boonstra 1984, Adler & Tamarin 1985), however, Desy & Thompson (1983) found adult males to be the main dispersers in spring. The high number of adult males in the ACW P. coucha population could reflect the immigration followed by maturation of both adult and sub-adult males. It is unlikely that the sub-adults present in the Session 5 population could have been born and matured to this extent on the trapping sites, therefore it seems the non-adult females might also have been a dispersing force.

P. natalensis also showed a high rate of increase in the ACW fifth session which, again, is not unexpected for one of the Praomys (Mastomys) species, however, it is also quite likely that immigration was important here too, although not to the same extent as for P. coucha. As the ACW habitat was a continuum of varying patch types and sizes, and not all were preferred by or acceptable to either P. coucha or P. natalensis (see Chapter 6) immigration from areas acceptable in the drought into areas which became acceptable as the grass conditions improved is not surprising. The likely source of immigrating individuals were the larger grassland patches. However, neither the source nor

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the dispersal patterns of either species over time or space were investigated in the present study.

In Session 6, differences in the population growth patterns of the three species were very obvious. While all species showed a cessation of breeding activity, a population increase can still be expected due to the recruitment into the trappable population of those young born or independent after Session 5. A healthy age structure at such a time should show a good proportion of non-adults in the population. Swanepoel (1972) found _S. campestris_ adults to predominate in the population in the spring with the age classes equally distributed in the summer and with sub-adults predominating in the winter. In the final session of the present study, during the winter season, the _S. campestris_ populations in both habitats not only showed a dramatic decline in total numbers but very few non-adults seemed to be present in the population. The age structures of the _S. campestris_ populations in Session 6 continued to suggest that the species breeding efforts were not successful. It is also possible, however, that large-scale emigration and/or heavy mortality of this species in particular was occurring. A specific and intensive study of the _S. campestris_ populations in the three months between Sessions 5 and 6 would have been necessary to assess and clarify these possibilities.

The _P. coucha_ populations both continued to show the largest rates of increase, however, the MKN population density and rate of increase were substantially higher than the ACW population. The ACW population had a slightly lower percentage of breeding animals in Session 5 which, to some extent, may account for the lower rate of increase. However, the largest difference in age structure between the populations was in the numbers of adult animals, not in the non-adults. While this suggests higher mortality of the adults in the ACW, the low mass gain of the non-adults between Sessions 5 and 6 showed that the age structure analysis may be presenting an incorrect picture of the true chronological age of the population. Accepting that the mass/age analysis may be inaccurate in this case, by far the most important implication of the non-adult mass gain results is that individual growth in the ACW may have become very stunted. This suggests that perhaps food was limiting (Cole & Batzli 1979, Desy & Thompson 1983) or social behaviour patterns had become inhibiting to individual growth of the ACW animals (Stueck & Barrett 1978, Porter & Dueser 1986).

The age structure diagram for the MKN population was probably fairly accurate as the 12 g mass gain for the non-adults was sufficient for advancement into the next age class. The large and equal proportions of adults and sub-adults with the lower proportion of juveniles represents a classic early post-breeding age structure. The fact that the non-adult mass gain in the post-drought was lower than in the drought does imply that some sort of limitation may have been starting in the MKN as well. However, this could also be attributed to slower growth of non-adult animals, especially those born late in the breeding season, as winter approaches (Schwarz, Pokrovski, Istchenko, Olenjev, Ovtschinnikova & Pjastolova 1964, Brown, E.B. 1973, Kaneko 1978, Malzahn 1981). The mass gain was still fairly large and so this may hint at greater limitations to come rather than significant limitations acting at that time. The slowing of the population growth of this species in the MKN appears more related to the intrinsically controlled factors, such as the length of the breeding season and genetically determined growth patterns (Schwarz *et al.* 1964, Malzahn 1981) rather than any strong extrinsic factor.

Population increase by *P. natalensis* in the ACW declined markedly after the high rate in Session 5, which was surprising as it had the highest percentage of animals still breeding in Session 5. The two *Praomys* species are evolutionarily and taxonomically very closely related. Assuming the two species have similar reproductive potential and strategy (Gordon 1984), the difference between the rates of increase in the ACW implies that greater limitation was being felt by the *P. natalensis* population than the *P. coucha* population. The age structure of the two *Praomys* species was very similar with high numbers of juveniles and sub-adults. The possibility that the *P. natalensis* age structure was also misrepresented seems likely. The continued total absence of adult females from the trapped *P. natalensis* population is extraordinary and the only explanation

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which can be suggested is one of differential trappability of or trap avoidance by the female segment of the population.

The sudden appearance of *P. natalensis* in the MKN in Session 6 was most likely a result of gradual but progressive dispersal from the original high population known to occur at Satara restcamp, 5 km away. The trapping of two juveniles shows that a breeding population was existing nearby.

The ability of *P. natalensis* to live commensally with man is well known (De Graaff 1981, Smithers 1983). During the drought, only *P. natalensis* existed in and around the camp itself while *P. coucha* was recorded in the surrounding veld (Gordon & Watson 1986). Rodent numbers in Satara also increased following the rains (pers. obs.) and further trapping in the surrounding veld then recorded both species, indicating that *P. natalensis* was dispersing. However, whether veld conditions had improved to the satisfaction of *P. natalensis* or densities were such in Satara to force dispersal is unknown. Interestingly, all the *P. natalensis* recorded in the MKN trapping areas were found in the trapping site closest to Satara (M2-5 km SE of Satara cf. M1-7 km ESE of Satara, see also Fig. 3, Chapter 2). This, plus the low numbers appearing at the M2 site suggests that the dispersing population had only just reached that area.

In conclusion, the population dynamics of these three species seem to reflect three stages of population regulation. First, during the drought, all populations attempted to breed within the normal breeding season but failed to produce an increase in population size. While intrinsic factors such as the length of the breeding season and the genetically determined male to female ratios are involved in delineating the breeding efforts of most small mammals (Wolff 1985a), it was apparent that these factors alone were not responsible for the lack of increase in my populations. The skewed sex ratios of the adults were not present in the non-adult populations, suggesting it was not an intrinsically controlled factor (i.e. genetically programmed skewed sex ratio from birth). Thus, as Wolff (1985a) found, the breeding efforts were restricted by various intrinsic factors but actually limited by various extrinsic factors, such as food, predators or suitable microhabitats.

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The second stage was in the early post-drought when the intrinsic factors again delineated the breeding efforts, which this time were highly successful for all species. This was probably due to release from the previously limiting factors as environmental conditions improved. Success was such that both reproduction and immigration (i.e. emigration from other more populated areas) were evident.

The third stage and also the more complex was the late post-drought, where both intrinsic and extrinsic factors working in density-dependent and -independent ways were observed. The intrinsically controlled length of the breeding season could have been the only regulating factor for the P. coucha population in the MKN. However, it was apparent that additional factors were influencing the ACW P. coucha population. Limited food, lack of suitable microhabitat space and/or greater predator pressure could all be involved as regulating factors. S. campestris was apparently being influenced by very different factors than the other two species. These factors, two of which seem to have been lack of breeding success and high mortality were such that the populations in both habitats fell almost below even the drought levels. The P. natalensis populations seemed to be influenced by different factors in the two habitats. As for P. coucha, the ACW P. natalensis population was probably being subjected to environmental limitations which were strongly influencing the rate of population growth. In the MKN, the population could only be explained as expanding into the area from elsewhere. The reasons for this dispersal could be intrinsically set social behaviours or tolerances or extrinsic environmental factors such as limited food in the originating area.

The following two chapters examine in greater detail the possible role of microhabitat availability and food as factors in regulating each of these populations in the two climatic periods.

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CHAPTER SIX

MICROHABITAT PREFERENCES AND AVAILABILITY FOR *SACCOSTOMUS CAMPESTRIS*, *PRAOMYS COUCHA* AND *PRAOMYS NATALENSIS*

INTRODUCTION

The role of microhabitat preferences and availability of such in the environment as possible population and community regulators has been a popular theme in small mammal studies of recent years (Price 1978 and references therein, Morris 1984). Microhabitat can influence small mammals in a variety of ways depending on the rigidity of each species's microhabitat requirements, the productivity and availability of specific microhabitats and the social tolerances of each species and community. Limitations in available space within preferred microhabitat conditions can restrict population sizes in essentially three ways. Maximum densities can be reached according to what is socially acceptable (intrinsic and density-dependent regulation), what is energetically supportable (extrinsic and density-dependent regulation) and what is predator-limited (extrinsic and usually density-dependent regulation). Depending on the environmental circumstances, these regulating mechanisms may be influential singly or in various combinations as they relate to the microhabitat requirements of each species.

To determine the microhabitat preferences of *S. campestris*, *P. coucha* and *P. natalensis* various microhabitat features were measured around each trapsite. These were grass and tree species diversity, variation in grass height, percentage grass cover, the density of trees in each of four height classes and the relative abundance of rocks, litter and forbs. A Kolmogorov-Smirnov goodness of fit test was used to test the occurrence of the various microhabitat features at the sites of each species's capture with what was randomly available in each habitat.

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Significant deviations from random occurrence identified the important features.

This chapter is structured such that the microhabitat variables important to the small mammals in the drought and post-drought periods are first identified. Then, because the environment itself is such a dynamic association between the biological and physical elements, the relationships between the distribution patterns of the important features is examined. This analysis showed that virtually all the important variables in each climatic period were significantly correlated to the percentage grass cover. The remainder of the chapter then focuses on the relationship between each species, its cover preferences and the cover availability in each trapping session. By comparing the preferences of each species with the availability of their preferred cover in each habitat and the maximum density attained by each species in their preferred cover conditions, an estimate of the importance of cover availability to each species is made.

If microhabitat availability alone is limiting the populations, one would expect the maximum density of each species in its preferred areas to be similar, regardless of habitat. Only the restraints of intrinsic social tolerances would determine density. However, if other factors, such as food availability or predators, were also influencing the populations then the maximum densities of each species in their preferred conditions may be different depending on the habitat.

METHODS & MATERIALS

Live-trapping Programme

The methods used in the live-trapping programme have been detailed in Chapters 4 and 5. Each trap and the 400 m^2 surrounding it was considered as a single point in space with its own unique combination of microhabitat features. While the exact location of the trap could have been further defined to a single

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microhabitat condition (e.g. beneath a tree, under grass, in the open), the larger area of 400 m^2 is used here because small mammals must travel to and from each trap and therefore, the area surrounding each trap may be equally if not more important than the actual trap location. Capture of an animal at a specific trap was interpreted as acceptance of the surrounding microhabitat conditions.

Microhabitat Assessment

Table 24 lists the microhabitat variables measured in the 400 m^2 (20 m x 20 m) plots surrounding each trap. Suggestions for the possible environmental and ecological significance of each variable to a small mammal are also listed. It must be emphasised, however, that these are only suggestions and are not being presented as the total or only interpretations which could be made.

Over the two year study period, some of the variables such as grass and tree species diversity, tree densities and rock abundance were unchanging and therefore, were only assessed once. The variation in their availability (Appendix III) depended on the number of trapnights that each trap was available to the small mammals in each session. Change in the amount of grass cover and the variation in grass height was a continual process, therefore, these variables were measured during each session. The general methods for assessing each variable are listed below the variable name. Further details on these methods may be found in Chapter 3.

The microhabitat variables were classified into low, medium and high categories (Table 24). The classification was kept as simple and as broad as possible for two reasons. First, how precisely each species can discriminate the condition of its environment was unknown. Therefore, it was better to underestimate their discrimanatory powers by keeping the categories broad rather than overestimate their abilities by distinguishing too many levels. Secondly, both the analyses and interpretation of the results are simpler and more direct with fewer categories.

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Table 24: The microhabitat variables measured at each trap station, their abbreviations (Abbr.), methods of assessment (see Chapter 3 for further details) divisions into catergories and suggested ecological significance to small mammals.

Abbr.	Microhabitat variable and method of assessment	Categories Low	Med.	High	Ecological Interpretation
GSD	Grass species diversity. Shannon's diversity index.	<0,33	0,34-0,65	>0,66	diversity in food and cover types/conditions
VGH	Coefficient of variation in grass height. Pasture disc meter.	<33%	34-65%	>66%	structural diversity of grass layer affecting cover conditions
%GC	Percentage grass cover. Pasture disc meter.	<33%	34-65%	>66%	cover from predators, amelioration of physiical environment
TSD	Tree species diversity. Shannon's diversity index.	<0,33	0,34-0,65	>0,66	diversity in food and habitat structure
TD0,5	Density of trees <0,5m. n/trap station (400 m^2).	<5	6-10	>10	source of cover & food but disrupts grass layer
TD1,0	Density of trees >0,5<1,0m. n/trap station.	<4	5-10	>10	source of food, little cover, disrupts grass layer
TD4,0	Density of trees >1,0<4,0m. n/ trap station.	<4	5-8	>8	source of food, no cover, grass layer not disrupted unless trees in high density
TD>4	Density of trees >4,0m. n/trap station.	<2	3-5	>5	source of food, no cover, grass growth inhibited, offer cover & perches for aerial predators
ROC	Rock distribution and abundance. 0=no rocks, 1=scattered small rocks, 2=few scattered larger rocks, 3=many scattered larger rocks, 4=scattered boulders, 5= large associations of boulders.	0&1	2&3	4&5	various forms of cover accumulations of plant and insect matter and water
LIT	Litter (plant debris no longer rooted in ground) distribution and abundance. 0=no litter, 1=isolated small patch, 2=small scattered amounts, 3=large scattered amounts, 4=discontinuous thick layer, 5=continuous thick layer.	0&1	2&3	4&5	same as above

continued overleaf ....

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FOR	Forb distribution and abundance. 0=no forbs, 1=few scattered forbs, 2=moderate scattered forbs, 3=abundant scattered forbs, 4=high coverage by forbs, 5=total coverage by forbs.	0&1	2&3	4&5	food source but usually little cover, occur where grass disturbed

Assessment of Preferences

To assess species preferences, the non-parametric Kolmogorov-Smirnov goodness of fit test was used to compare the frequency of variables (i.e. microhabitat conditions) present at traps where the three species were caught with the availability of the same over the traplines. Significant deviations in use from the proportional availability in the environment identified the important microhabitat features. Within each important feature the category (low, medium or high) which showed the greatest proportional difference (positive or negative) from the general availability identified the preferred (positive) or avoided (negative) condition.

Only the capture records from animals caught more than once were used in an effort to exclude transient individuals (Grant 1970). Multiple captures of the same individual, however, were used as separate data points based on the premise that an individual uses its home range in the same manner as the species would use the general habitat, that is, areas with more suitable conditions will be used more often than areas with less suitable conditions.

To increase sample size and in the belief that microhabitat preferences and priorities may have changed with the changing environmental conditions, preferences were ascertained for the drought period by grouping data from Sessions 1 to 4 and for the post-drought period by grouping data from Sessions 5 and 6. The Kolmogorov-Smirnov goodness of fit test when used on grouped data becomes highly conservative, increasing the chances of a type II statistical error (Zar 1984). While this is unfortunate, the statistical error is such that I would increase the chances of not detecting a microhabitat preference rather than incorrectly concluding there was a preference when there was none. Therefore, when a microhabitat preference is indicated, it can be accepted with confidence.

From the statistical analyses, one must interprete the ecological significance of the positive or negative signs in the proportional use of the different microhabitat features. In the present study, positive selection for a condition is accepted as a straightforward, active choice for that condition. Avoidance, however, may have more subtle interpretations as statistically speaking, the negative proportional difference could become the largest proportional difference in two ways. First and simplest is that the species's primary goal is to actively avoid a certain condition, for instance low cover. This implies that being in either of the other two conditions, namely medium and high cover, is acceptable as long as the low cover is avoided. This assumes then that no great difference in the proportional use of the other two categories is evident and therefore, that there is no preference between them. Thus, where avoidance was shown, the proportional differences of the other two conditions of the variable were examined to see if the rodents showed any preference between them.

If a preference between the other two conditions was evident, then the question arises as to whether this is a true secondary preference, that is a subsequent preference after active avoidance of one condition or whether in fact it is active selection for the "secondary preference" but, for one reason or another, the density of animals using the preferred condition was at a maximum and so the surplus were forced to increase numbers in the next best condition. In terms of the Kolmogorov-Smirnov test, this overflow of animals into a second best condition would in effect dilute the strength of the proportional difference of the first choice condition and leave the negative proportional difference as the largest, creating the statistical impression of avoidance. Continuing with the previous example of cover preferences, the impression of strong avoidance of low cover conditions would result if the animals actively avoided low cover (active avoidance) or had a strong preference for high cover but possibly some other factor was limiting (e.g. social space or food) such that the preferred condition was insufficient for the number of animals wanting to reside there, creating a number of surplus animals. If the excess animals then moved into the medium cover as the next best alternative. This would result in what I would call passive rather than active avoidance of the low cover. Passive avoidance then would be a result of density-dependent effects on microhabitat selection, a situation which has been postulated and shown to occur in other studies (M'Closkey 1981, Morris 1984, Adler 1985).

Most of the variables shown to be important were correlated to the availability of the different grass cover levels. To explore whether cover availability was limiting the species densities, the availability of cover was assessed in each session by calculating the proportion of traps in each cover level. By assuming that the distribution of cover conditions among the traps was a reasonable reflection of conditions in the general vicinity of the traplines, the total area (within each estimated A_t, see Chapter 4) over which each cover condition existed was estimated by multiplying the A_t by that proportion of traps. For example, if the A_t was 30 ha and the proportion of traps with low, medium and high cover was 0,61, 0,25 and 0,14 respectively, then the estimated area of low cover conditions was 30 x 0,61 = 18,3 ha with the areas of medium and high cover being 7,5 and 4,2 ha respectively.

The utilisation of each condition by the different species was calculated by counting the number of individuals (resident and transient because they would both use food and space) in each session captured in the different cover conditions and dividing it by the estimated area. This provided a density value I call the utilisation density. If an individual was captured at a number of traps which were classified into more than one of the cover conditions then, depending on whether it was caught in two or all three of the conditions, 1/2 or 1/3 of an animal was accorded to each condition it was trapped in. Continuing with the previous example, if 72 S. campestris were captured on the trap lines and 35 of the animals were in low, 30 in medium and 7 in high cover, then the utilisation density of each cover type by S. campestris would be 1,9 (35a / 18,3ha of low cover), 4,0 and 1,7 a/ha respectively. Thus the maximum density the species was able to attain in its preferred microhabitat condition and under the environmental conditions at the time was 4,0 a/ha as compared to an overall habitat density of 72a/ 30ha = 2,4 a/ha.

RESULTS

During the drought, the important microhabitat variables in each habitat were fairly similar. Grass species diversity (GSD), percentage grass cover (%GC), the density of small trees (TD0,5) and forbs (FOR) were important in both habitats (Table 25). In addition, litter (LIT) was important in the MKN while variation in grass height (VGH) was important in the ACW. There was a greater number of and consistency in the variables which were important to species in the MKN than in the ACW. That is, what was important to *S. campestris* in the MKN was generally important to *P. coucha* as well. However, in the ACW, fewer variables were important and none were important to more than one species. In the post-drought, the situation was reversed. There were fewer variables important in the MKN, however, consistency in the importance of specific variables between species was much the same.

The fact that some of the non-changing variables were important in one climatic period and not the other suggests that those variables themselves may not have been the important feature but just that their distributions in the different climatic periods may have been correlated to another more dynamic feature. Table 26 presents a correlation matrix of all the variables in each climatic period and in each habitat. In the MKN during the drought GSD, FOR and TD0,5 which were all shown to be important variables to the small mammals, were inversely correlated with grass cover but were not correlated with each other. That is, where grass cover was highest, GSD, TD0,5 and FOR were lowest but the distributions of the latter three variables were independent of each other, except for LIT and FOR being positively correlated to GSD.

Table 25: Microhabitat preferences (Kolmogorov-Smirnov test, $P<0,05$) of *Saccostomus campestris*, *Praomys coucha* and *P. natalensis* during drought and post-drought conditions in the MKN and ACW landscapes of the KNP. The microhabitat variables TSD, TD1 and ROC did not show a significant relationship with any species therefore, these variables have been excluded from the table. += selection for, -= avoidance of. L, M, H= low, medium and high categories respectively which were significant. Where avoidance was the strongest association and a preference among the remaining two categories was evident, then the more preferred category is indicated in (). ns - shows an association as would be expected by random availability. ^{a}= medium cover was the highest cover available at the time. --= species not present at that time.

	Drought		Post-Drought	
	MKN	ACW	MKN	ACW
S. campestris				
GSD	+L	ns	ns	ns
VGH	ns	ns	ns	ns
%GC	+M^a	ns	-H (+M)	ns
TD0,5	+L	ns	-L (+M)	+M
TD4	ns	ns	ns	ns
TD>4	ns	ns	ns	ns
LIT	ns	ns	ns	ns
FOR	+L	+L	ns	ns
P. coucha				
GSD	+L	ns	ns	-H (+M)
VGH	ns	ns	ns	-H
%GC	+M^a	+M^a	+H	-L (+H)
TD0,5	ns	ns	ns	-L (+H)
TD4	ns	ns	ns	-H (+L)
TD>4	ns	ns	ns	+L
LIT	+L	ns	ns	ns
FOR	+L	ns	ns	ns
P. natalensis				
GSD	--	+H	ns	ns
VGH	--	+H	ns	ns
%GC	--	ns	ns	+H
TD0,5	--	+H	ns	+H
TD4	--	ns	ns	ns
TD>4	--	ns	ns	ns
LIT	--	ns	ns	ns
FOR	--	ns	ns	+H

In the post-drought period, again the variables shown to be important to the three species in the MKN were inversely correlated to grass cover. VGH, which during the drought showed no correlation with grass cover, after the rains showed a significant negative correlation (Table 26a). This would be

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expected as the grass layer became more uniform after the rains (Chapter 3).

Table 26: Mean drought (above diagonal) and post-drought (below diagonal) period correlation coefficients of the intra-landscape microhabitat variables in the MKN (A.) and ACW (B.) landscapes of the KNP. Microhabitat variables GSD to FOR were non-changing between climatic periods and therefore, are reported only once yet, the results apply to both periods. Due to the large sample sizes (MKN n=165, ACW n=166), even low correlations were significant therefore, the P<0,001 (r>0,256) level of significance was used to show only the strongest of correlations.

A.	%GC	VGH	GSD	TSD	TD0,5	TD1	TD4	TD>4	ROC	LIT	FOR
%GC		ns	-0,42	ns	-0,33	ns	ns	ns	ns	ns	-0,42
VGH	-0,35		ns	+0,45	ns	ns	ns	ns	ns	ns	ns
GSD	-0,32	+0,29		ns	ns	ns	ns	ns	ns	+0,31	+0,36
TSD	ns	ns			ns	ns	ns	+0,30	ns	ns	ns
TD0,5	-0,35	ns				ns	ns	ns	ns	ns	+0,29
TD1	ns	ns					ns	ns	ns	ns	ns
TD4	ns	ns						ns	ns	ns	ns
TD>4	ns	ns							ns	ns	ns
ROC	ns	ns								ns	ns
LIT	ns	ns									ns
FOR	-0,47	+0,46									

B.	%GC	VGH	GSD	TSD	TD0,5	TD1	TD4	TD>4	ROC	LIT	FOR
%GC		ns	ns	ns	ns	ns	ns	-0,32	ns	ns	ns
VGH	-0,51		ns	ns	ns	ns	ns	ns	ns	ns	ns
GSD	ns	ns		ns	ns	ns	ns	ns	ns	ns	ns
TSD	ns	ns			ns	+0,26	ns	ns	ns	ns	ns
TD0,5	+0,29	ns				ns	ns	ns	ns	ns	ns
TD1	ns	ns					ns	ns	ns	ns	ns
TD4	-0,31	ns						ns	ns	ns	ns
TD>4	-0,43	ns							ns	ns	ns
ROC	ns	ns								ns	ns
LIT	ns	ns									ns
FOR	ns	ns									

In the ACW during the drought there was only one significant correlation amongst the important variables, that of the density of trees greater than 4,0 m (TD>4) being inversely correlated with grass cover (Table 26b). Following the rains, more significant correlations were apparent, however, all were associated with grass cover. VGH, TD4, and TD>4 were all negatively correlated while TD0,5 was positively correlated with grass cover. Again, VGH, TD4, TD>4 and TD0,5 were independent of each other.

The important microhabitat variables to S campestris in the drought conditions of the MKN were all negatively correlated with grass cover (Tables 25 and 26). Low GSD, TD0,5 and FOR conditions occurred where grass cover was highest, suggesting that the ultimate feature was the grass cover. In the ACW, cover did not seem to be important as only a selection for low forbs was significant.

Cover was important to P. coucha in both habitats during the drought and again all the other variables important in the MKN, except litter, were negatively correlated with grass cover (Tables 25 and 26). In the ACW, despite their low numbers, P. coucha showed a significant association with high cover. No other significant microhabitat association was apparent. As grass cover in the ACW at that time was not highly correlated with any of the other variables, except large trees, this again emphasises the importance of cover as a primary microhabitat feature for this species.

P. natalensis showed the greatest number of important microhabitat variables for the ACW habitat during the drought and each one stressed heterogeneity in the grass layer (Tables 24 and 25). These animals (only 5) were closely associated with the scrub thickets which occurred around the edges of the dry vleis and streambeds. These areas had a highly variable grass layer, which did not provide much grass cover, however, the scrub thickets still provided good aerial cover.

Under the post-drought conditions, S. campestris was still fairly undemanding of its environment, as I measured it, with only a preference for a medium density of small trees being important (Table 25). Small trees were important in both habitats. In the MKN, S. campestris also avoided high cover while preferring the medium cover conditions. The avoidance of high cover and low TD0,5 with preferences for the medium condition in both variables again may reflect the negative correlation between them. However, the similar selection in the ACW (+Med.) suggests that the small trees may have been important in their own right (Tables 25 and 26).

P. coucha, as before, showed a selection for the highest cover available (Table 25). In the ACW the strongest association was an avoidance of low cover, however, this seems to have been passive avoidance as a secondary selection for high cover was evident. Many of the microhabitat variables important to P. coucha in the ACW post-drought sessions showed significant negative correlations with grass cover, thus again emphasising the primary importance of this feature.

P. natalensis did not show any significant associations with any microhabitat variables in the MKN (Table 25), but then with so few animals in this habitat it is not surprising. P. natalensis in the ACW post-drought, associated with the highest grass cover conditions as did P. coucha but P. natalensis also showed preference for high densities of forbs, a feature not correlated to grass cover (Table 26).

Because the microhabitat preferences of the species seemed to emphasise aspects of cover and grass cover was one of the most dynamic variables, the availability of the different cover conditions in each session and habitat was hypothesised to be a limiting factor for these species. To explore this the density of each species using the different cover levels was examined.

Low grass cover conditions predominated over both landscapes in the drought, with no high cover available at any time (Table 27). Maximum densities of S. campestris and P. coucha, occurred in the medium cover areas, nevertheless, the densities were still very low. Both S. campestris and P. coucha showed maximum densities during the drought in the medium cover areas in the Session 3 winter season. The availability of medium cover in was more restricted in both habitats during Session 3 than at any other time in the drought period. Thus while the number of animals did not increase at this time, the utilisation densities did because the animals were concentrating their movements in the smaller medium cover areas available.

Conditions in Session 5, about 2-3 months after the rains returned, were considerably improved. In both habitats, medium cover predominated, however, there were larger areas with low and high cover available in the ACW habitat (Table 27). With the

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changes in cover availability, different density utilisation patterns for the three species emerged. In the MKN, S. campestris showed heavier utilisation of the medium and low cover areas. This is a slight contradiction of the S. campestris microhabitat preferences shown in Table 25, however, this probably results from the inclusion of information from 'transient' animals in the calculation of utilisation densities. Nevertheless, the low utilisation of the high cover areas was apparent. In the ACW, the utilisation densities were fairly even, however, the preference for medium cover was still evident. In both habitats, the maximum density which was attained or tolerated was similar, at approximately 6,6 a/ha.

P. coucha showed similar utilisation patterns in both habitats with hierarchical use of the three cover levels (Table 27). Maximum use was made of the high cover areas, however, there was a large difference in the densities and the ratio of useage. In the MKN, the ratio of low to high cover useage was 1: 1,8: 3,3, while in the ACW it was 1: 3,3: 6,9, suggesting a higher degree of selection in the ACW. Maximum density attained or tolerated by P. coucha was 15,7 a/ha in high cover.

P. natalensis densities were still quite low in Session 5, however, the species did show a slight preference for medium cover in the ACW (Table 27).

By Session 6, the population sizes of the three species had changed considerably (Fig. 18, Chapter 5) as had the relative availability of each cover type (Table 27). In the MKN, there was a shift to a greater relative amount of high cover. The ratio of cover availability changed from 1: 6: 2 (low: medium: high) in Session 5 to 1: 15: 9 in Session 6. In the ACW, availability remained essentially equal, however, the emphasis shifted from medium to low cover. The availability ratio changed from 1,1: 1,4: 1 in Session 5 to 1,4: 1,1: 1 in Session 6.

Following the crash of the S. campestris MKN population, all individuals (only 3) were captured in medium cover areas, which gave a maximum utilisation density of 0,4 a/ha (Table 27). This was well below what the species was able to tolerate in any cover condition found in the previous session or even during the drought. S. campestris density in ACW was also low, however, their maximum density at 1,8 a/ha in the low cover areas was a bit higher than in the MKN. This was still much lower than the maximum densities of the previous session.

Table 27: Utilisation density of *Saccostomus campestris* (Sc), *Praomys coucha* (Pc) and *P. natalensis* (Pn) in the three grass cover conditions, low (<33%), medium (34-65%) and high (>66%), in the MKN and ACW landscapes of the KNP. The estimated area (ha), within the area of trapping effect (see Chapter 4) covered by each cover condition is given. ES, LS and W as before.

	MKN				ACW			
	ha	Sc	Pc	Pn	ha	Sc	Pc	Pn
Session 1 (ES)								
Low	23,4	0,7	0,2	0,0	20,4	0,4	0,0	0,0
Medium	5,9	0,9	0,1	0,0	8,4	0,8	0,0	0,0
High	0	---	---	---	0	---	---	---
Session 2 (LS)								
Low	31,3	0,4	0,4	0,0	21,1	0,9	0,0	0,0
Medium	13,4	0,7	0,6	0,0	4,9	0,8	0,0	0,0
High	0	---	---	---	0	---	---	---
Session 3 (W)								
Low	22,3	1,2	1,1	0,0	20,8	0,6	0,1	0,1
Medium	1,4	2,1	4,6	0,0	1,6	1,6	0,0	0,0
High	0	---	---	---	0	---	---	---
Session 4 (ES)								
Low	26,5	0,8	1,2	0,0	28,3	1,2	0,1	0,2
Medium	4,3	1,4	1,4	0,0	3,3	0,8	0,0	0,0
High	0	---	---	---	0	---	---	---
Session 5 (LS)								
Low	2,0	6,5	4,7	0,0	5,9	3,8	0,8	0,5
Medium	11,9	5,0	8,4	0,0	7,6	6,7	2,7	1,0
High	4,1	2,6	15,7	0,0	5,4	4,8	5,5	0,7
Session 6 (W)								
Low	0,5	0,0	29,0	0,0	5,8	1,8	3,3	1,1
Medium	7,4	0,4	29,9	0,4	4,6	0,4	10,1	3,3
High	4,4	0,0	30,0	0,7	4,0	0,9	12,4	5,1

P. natalensis showed maximum densities in the high cover areas of both habitats, with the highest density of 5,1 a/ha occurring in the ACW (Table 27).

For the first time, *P. coucha* population in the MKN showed

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equal useage of all three cover types with extremely high densities around 29-30 a/ha in each one (Table 27). In contrast, the ACW population still showed the hierarchical use of the three cover types. The maximum density of P. coucha supported in the ACW was 12,4 a/ha under the high cover conditions. This was well below the socially tolerated 29-30 a/ha seen in the MKN.

DISCUSSION

Many of the variables chosen to examine the importance of various features in the grass and woody plant community were found to be correlated with grass cover. Because the plant community as a whole is very dynamic, such correlative relationships can be expected to occur. Competition, especially for light, between grasses and trees and also between grass plants is well documented (Went 1973, Gadgil & Gadgil 1975). In the present study, among those variables shown to be important to the rodents in the MKN, grass species diversity, abundance of forbs and the density of small trees ($\leq$0,5 m) were all negatively correlated with grass cover. The significant correlations in the MKN did not change very much with the return of good environmental conditions.

The ACW showed very few microhabitat correlations in the drought conditions, however, as the grass community recovered, more correlations appeared. The general lack of correlations between the variables in the ACW reflects the inherent heterogeneity of this habitat. Those variables which showed significant correlations after the rains seemed to reflect competition between the grasses and trees. The high densities of larger trees (>1,0 m) tended to inhibit grass growth and thus grass cover beneath them, while the density of small trees and grass cover were positively correlated. While this may suggest that small or young trees were also inhibited by the larger trees, a negative correlation between the large and small trees was not evident. Rather, this positive correlation between grass cover and small trees reflects the distinct tree species composition in the three patch types (see Appendix II).

The consistency in the importance of grass cover in both habitats and both climatic periods, plus the fact that most of the other variables shown to be important were generally correlated with grass cover suggests that grass cover may be the overriding environmental influence in small mammal existence in these two habitats. Kern (1981) also suggested that cover was of primary importance to the small mammals he studied in the KNP while many other studies both in Africa (Swanepoel 1972, Cheeseman & Delaney 1979, Rowe-Rowe & Lowry 1982) and elsewhere (Goertz 1964, Grant, Birney & Baird 1976, Grant & Birney 1979, Grant & Morris 1971, Spencer & Cameron 1983, 1985) have shown similar results. The correlation of so many of the other variables with grass cover, however, serves as a reminder that even cover may not be the important feature but perhaps a correlative of cover which was not measured in the present study (Batzli 1968). For instance, soil seed reserves have been shown to be highest where plant cover was greatest (Nelson & Chew 1977, Parmenter & MacMahon 1983, but see Price 1978) and also physiological conditions such as temperature and humidity are greatly ameliorated under dense grass (Getz 1961a, 1961b and references therein, Parmenter & MacMahon 1983).

Numerous microhabitat preferences were apparent in both climatic periods. S. campestris showed a consistent selection for medium cover in the MKN, however, in the ACW, the species showed very few preferences. The lack of a consistent microhabitat preference between habitats supports the wide habitat tolerance which is reported for this species in the literature (De Graaf 1981, Smithers 1983). In the ACW, grass cover itself did not seem to be important. This could suggest that there was less predator pressure in the ACW, hence cover was not such a necessity or perhaps that food was less tightly associated with the grass clumps in the ACW than in the MKN. The post-drought association with small trees in both habitats may reflect their importance as a food source to this species. While primary production by the grasses was readily available to the small mammals early in the post-drought, only the small tree species had recovered sufficiently by the late post-drought to have produced seeds which were potentially available as a food source (see Chapter 3).

In contrast to the variable microhabitat preferences of *S. campestris*, *P. coucha* showed a consistent preference for high cover in both habitats. The interesting pattern here lies in the positive selection for high cover in the MKN, even when densities were high, and the avoidance of low cover in the ACW. The avoidance, however, was interpreted as passive because a preference for the high cover and its associated correlates was evident. This implies that the availability of high cover may have been limiting the ACW *P. coucha* population. The avoidance of a highly variable grass layer was the only avoidance situation which could be interpreted as an active avoidance, however, as this variable was negatively correlated to grass cover, it still may not have been a case of true active avoidance.

The microhabitat preferences of *P. natalensis* seemed less consistent than those of the other species. No preferences were shown in the MKN rain period, however, with the low number of individuals this is not surprising. Despite the low numbers in the ACW drought, *P. natalensis* showed preferences for a heterogenous grass layer, however, these results can not be interpreted too rigorously due to the small population. A few observations on the species distribution when a small population was present are relevant here because the ACW drought population and the MKN sixth session population showed some common traits. First, both populations were rather clumped in their distribution and perhaps the overriding factor here was a close social association rather than a microhabitat association. Secondly, the *P. natalensis* trapped in the ACW drought were always found in the lower-lying areas around the dry vleis and streambed of the A1 trapping site, while four out of six in the MKN post-drought were captured near the small vlei in the M2 trapping site (refer Figure 7, Chapter 2). In addition, during the drought, *P. natalensis* occurred in its greatest numbers around Satara where the water table was abnormally high (see Chapter 2). Whether this is significant or not is unknown, however, it does suggest that other environmental features may have been of greater importance to *P. natalensis* than the ones measured in the present study. Smithers (1971) has suggested that P. natalensis may be dependent to some extent upon water. Following the rains, P. natalensis in the ACW spread over the whole habitat and was apparently dispersing out from Satara into other areas of the MKN. The microhabitat preferences recorded in the post-drought were similar to P. coucha. Interestingly, the preferences shown by P. natalensis were all positive selection for rather than passive avoidance of the variables shown for P. coucha which may be evidence for density-dependent effects on microhabitat selection as hypothesised by M'Closkey (1981) and Morris (1984).

Comparison of the microhabitat preferences of this species with that reported in the literature is complicated by the only recent recognition of two species. One cannot be sure that the reported preferences are for P. natalensis or for P. coucha, however, knowledge of the present distribution of the two species does help (Green, Keogh, Gordon, Pinto, & Hartwig 1980). While ecologically the two species are very similar (Green, Gordon, & Lyons 1978) the results of the present study show that different factors may influence the two species, especially under environmentally stressful conditions. Both Sheppe (1973) and Smithers (1983) note that P. natalensis occurs around the fringes of dry waterways, while others have often noted it as a pioneer species, frequenting areas with high plant diversity and a high proportion of weeds (Meester, Lloyd, & Rowe-Rowe 1979). This description agrees well with the microhabitat preferences found for the species in the ACW during both climatic periods. Interestingly, it does not fit with the microhabitat preferences shown by P. coucha in either habitat suggesting that perhaps P. coucha is less of a pioneer species than P. natalensis.

If all the elements essential to survival are in superabundance within each cover condition, or at least within the preferred cover conditions of each species, then one would expect the density of each species in its preferred condition to increase to the maximum level which was socially acceptable. In addition, one would expect maximum densities to be reached in a hierarchical manner with densities peaking in the preferred condition first and the least preferred condition last (Fretwell 1972 and references therein). Thus the association between animal distribution and the distribution of the microhabitat features would tend to weaken as animal density increased (Grant & Morris 1971, Morris 1984).

The maximum densities of all three species in their preferred cover conditions were encountered in the post-drought period. S. campestris showed a maximum density of 6,7 a/ha in medium cover while P. coucha associated at a density of 30 a/ha and P. natalensis at a density of 5,1 a/ha in high cover. Assuming that the inherent social tolerances of each species is the same in both habitats and that the maximum densities found in the post-drought were not grossly exceeding the tolerance of any species, then it would appear that, during the drought, cover alone should not have been a limiting factor for any species. Although the availability of medium and high cover during the drought was limited, the densities of animals using those conditions were well below the tolerated social levels observed later. These results strongly suggest that another essential resource or combination of resources such as food and/or water was not in super-abundance or that the cover which was available was just not sufficient to protect the small mammals from predators.

Under the unlimited population growth conditions observed in Session 5, one would expect the utilisation densities to be arranged in an hierarchical manner. This situation was exactly what was observed. P. coucha, which had the most restricted and consistent cover preferences, is a classic example of such a hierarchical pattern. S. campestris concurs with its suggested cover preferences in the MKN by showing a low utilisation of the high cover areas, however, the secondary preference for medium cover does not show up. It was suggested that this may have been due to inclusion of cover useage by transient individuals as well as resident animals. Comparing the cover preferences of the resident animals with the cover utilisation densities suggests that there may have been a large number of transients in the S. campestris populations. The resident animals, in the medium cover areas may have been forcing the transients into the low cover conditions. Numerous authors have shown that transient or subordinate individuals are often forced to use non-preferred microhabitats when densities become high (Grant 1970, Madison 1980, Spencer & Cameron 1983). This could suggest that the species was close to it's social tolerance. S. campestris is well known for it's high intra-specific aggression (Choate 1972, Earl 1980, Smithers 1983). In the ACW, S. campestris showed highest use of the medium cover and roughly equal use of low and high cover. This tends to agree with the apparent reduced importance of cover to the species in the ACW habitat.

Session 6 showed the greatest changes in species population patterns. Based on the tolerated densities in Session 5, the availability of medium cover alone cannot account for the crash of the S. campestris populations in either habitat. Notably, the highest density useage in the ACW population had switched from medium cover to low cover, suggesting that medium cover, for some reason, was not as suitable as it once was.

The P. natalensis densities in the fifth session showed almost equal useage in all cover conditions but the densities were really too low to reveal any definite pattern. P. natalensis density increased in Session 6 but at a slower rate than in the previous session. The species during Session 6 showed the hierarchical pattern of cover use, however, it is unlikely that P. natalensis would have reached its social limits at just 5,1 a/ha as this species is known for its reproductive capabilities and population explosions have often been noted in the literature (De Graaff 1981). While the low rate of population increase, when compared to P. coucha, implies some limitation, these results, although not conclusive, suggest that cover alone was not the limiting factor.

The cover utilisation densities of P. coucha in the MKN sixth session no longer showed the hierarchical pattern of use of preferred conditions but equal useage of all conditions, as would be predicted from the models by Grant & Morris (1971) and Fretwell (1972). Grant & Morris (1971), however, warn against overly easy acceptance of equal useage under high density conditions and it must be recognised in the present study that the appearance of equal useage may have been an artifact of the 95% trapping success. With the number of traps limited, there may have been greater numbers of P. coucha in the high cover areas but there were just no traps available to capture them. Indeed, this is very likely to be true, however, the large numbers of animals using the low and medium cover areas still suggests an overflow situation. If the utilisation densities do reflect a true situation, then this suggests three things. First, that P. coucha can actually survive at equal densities in the low, medium and high cover conditions. Secondly, that possibly the social limits of the species may be around 30 a/ha or that 30 a/ha may be maximum supportable P. coucha density under the MKN post-drought conditions, again however, this may also be a reflection of trap saturation. And thirdly, if this species can equally utilise all three cover conditions, then perhaps cover itself is not the ultimate microhabitat variable. Perhaps the species is dependent upon something else which was strongly correlated to cover.

I would suggest that during the post-drought period of this study, cover was not limiting the MKN P. coucha population, however, it appears that perhaps either social or food limitations were approaching. Although the ACW P. coucha population was showing signs of limited population growth, (Chapter 5), it does not seem likely that the availability of cover was a major limiting factor. The socially tolerated densities in the MKN were 2,5 times greater than in the ACW and the continued hierarchical use of the cover conditions in the ACW do not suggest that there was a large social overflow of animals.

In conclusion therefore, cover alone did not seem to the the major limiting factor for any of the species during the drought period. The maximum densities observed in the drought were well below the socially tolerated densities in the post-drought period, however, cover may have been secondarily involved in limiting the populations through insufficient cover and increased predator success. With increased density after the rains, all species tended to show the hierarchical use of preferred cover conditions, however, again cover availability alone could not explain the population decline of S. campestris or the much lower rates of increase by the two Praomys species in the ACW. Only in the MKN P. coucha population could cover possibly be evoked as limiting the species's maximum density, although this could also

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be explained by trap saturation.

The following chapter examines the food preferences and body condition of the small mammal communities in the two climatic conditions to explore the potential role of food as a limiting factor.

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CHAPTER SEVEN

RELATIVE COMPOSITION OF THE DIET AND BODY CONDITION

INTRODUCTION

Small mammal species are generally categorised into four or more consumer groups or guilds, based on their food type preferences. Those that eat primarily seeds as granivores, green vegetation consumers as herbivores, insect consumers as insectivores and combinations of the above three as omnivores (Grant & Birney 1979). It is not often, however, that members of each guild feed exclusively within strict food categories but merely use greater proportions of different food types as environmental conditions allow. Different food preferences or shifts in the proportional use of the food categories facilitate the coexistence of those species and individuals comprising a small mammal community. Changes or differences in the diet composition may reflect seasonal availabilities (Watts 1968, Field 1975, Neal 1984, Cole, Loope & Medeiros 1986), microhabitat affinities (M'Closkey 1985, Harris 1986), or major changes in the small mammal community structure (Brown & Lieberman 1973, Meserve 1976, Trombulak & Kenagy 1980, Brown & Munger 1985). Depending on the cause of the dietary shift, consequential changes in the amount of body fat may occur (Lidicker 1973, Cole & Batzli 1979). Changes in diet composition and body fat, individually as well as in conjunction with each other, can be indicative of changes in population stress levels.

It was in this light that diet composition and percentage body fat, an indicator of general body condition (Young 1976), were investigated in this study. As shown previously, the drought disrupted the usual seasonal weather patterns and the vegetation and small mammal community responses could be grouped into drought and post-drought periods (Chapters 3, 4, 5). Environmental stress was undoubtably high during the drought period as primary production failed and cover remained sparse after the burning. Small mammal population growth was limited and mortality apparently high. Under these conditions, changes in the diet composition of the small mammal species may have been necessary to ensure survival in the altered habitat. Depending on the nutritional quality and the quantity of the food available to the small mammal community, body condition may or may not be affected. This chapter investigates diet composition and body condition during the drought and post-drought periods.

METHODS AND MATERIALS

Snap-trapping Programme

Limited snap-trapping of animals was undertaken during the drought to obtain samples for stomach content analysis and fat extraction. Snap-trapping was performed in May/ June 1983. Due to timetable restrictions caused by the live-trapping schedule, snap-trapping was necessarily included a full moon period, although the two days either side of full moon were avoided. All snap-trapping was undertaken at least 2 km away from the live-trap areas. None of the animals killed in the snap-trapping had been previously marked on the live-trap lines. Because the only object of the snap-trapping was to obtain specimens for diet and fat analysis, the location of the snap-trap lines in each habitat was moved often to maximise trapping success. Snap-trapping was run concurrently in both habitats and the length of trapping in any one spot varied from three to seven nights. Single census lines were set with both a museum special and a victor trap at each trap station. The length of the lines varied between 10 and 15 traps per line with approximately 20 m between traps. In total, there were 573 trap nights in the MKN and 443 trap nights in the ACW. It was suggested by the Research Division of the KNP that a maximum limit of 20 animals per habitat could be sacrificed. All animals captured were taken back to the field camp, weighed, reproductive condition assessed, various morphological measurements taken (see Appendix III), stomachs

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were removed and in the case of Praomys species, blood samples were taken.

Stomach Content Analysis

Each stomach was removed and the contents emptied onto two clear petri-dishes. Water was added and the mixture gently swirled until the stomach contents were separate and uniformly distributed. Excess water was then removed with a pasteur pipette. Three 60mm lines were drawn randomly on the bottom of each petri-dish and then each line was examined at 10X magnification under a light microscope. The number of black, white and green or cellularly structured particles touching each line was recorded. In each stomach the percentages of black, green and white particles, interpreted as insect, vegetation and seed matter respectively, were then calculated by dividing the number of each particle type by the total number of particles counted (Grant *et al.* 1977, Kern 1981). The diet composition results within species were averaged to provide species mean values. It must be cautioned here that due to the instantaneous nature of the sampling method combined with the very low sample sizes all diet results should be treated as indicative only. An atypical night of foraging for any individual prior to being caught could have a disproportionately large influence on the species mean values. Various community trends in the diet composition are identified during the drought period. However, stomach content analysis was not undertaken in the post-drought period due to the restrictions on the number of animals which could be sacrificed. It was decided that the quota of sacrificed animals would be better used in validating the tritiated water methodology described below. Although post-drought diet results were then lacking, the diet results from Kern (1981), taken from the small mammal communities in the MKN habitat during the good rainfall periods of the late 1970's, are presented to provide a simple comparison of the diet composition during the two extremes in environmental conditions.

Fat Analysis

Direct fat extraction

Following stomach content analysis, each carcass was placed in an individual container and kept frozen until it could be dessicated in a freeze dryer. Whole carcasses were dried until 50% of the original mass had been lost (as measured on a Mettler balance, sensitivity to 0,001 g) and then coarsely chopped up by knife and freeze dried again. When mass loss stabilised, the chopped carcasses were finely ground in a commercial electric coffee grinder and again returned to the freeze drier. The final dry body mass was used to calculate total and percentage body water.

Fat extraction by petroleum ether was conducted in a Soxhlet apparatus (Harris & Kratochvil 1981). Prior to extraction, all fat collection flasks were dried in a 70^{o}C oven overnight and then weighed. Extraction samples, varying in mass from 1 to 6 g, were folded into a piece of filter paper, placed in extraction thimbles and subjected to extraction for a 16 h period. This time period was well in excess of the 3 to 6 h necessary for complete fat extraction in petroleum ether (Dobush, Ankney, & Krementz 1985). After extraction, the thimbles were removed and the excess petroleum ether was collected in the upper chamber and poured off. The collection flasks, containing the remaining small amount of petroleum ether and the extracted fats, were again placed in a 70^{o}C oven overnight. Each dried flask was then reweighed and the initial and post-extraction mass difference represented the extracted fat mass from that sample. Total fat mass (g) in each animal was determined, either from extraction of the whole body or, in the case of the larger animals, by extrapolation from the percentage fat in the combined sub-samples to fat mass of the initial dry body mass. Two to four samples per animal were extracted depending on the original size of and the degree of variability calculated in the dry body percentage of fat for each animal. If the calculated percentage fat varied by more than 1% between sub-samples, subsequent samples were run until either the whole animal was used or a difference of less than 1% was obtained.

Total fat mass was also used for the determination of the total body water (TBW) to body protein or lean body mass (LBM) ratio (Holleman, White & Luick 1982). This ratio is accepted as approaching a constant value, 0,732, for all species as they reach chemical maturity or, in other words, adulthood (Pace & Rathburn 1945). However, Holleman & Dieterich (1975), working with wild caught North American rodents, reported a value of 0,716. Because a value for this ratio has not been calculated for African rodents, TBW/LBM ratios were determined for all animals whose TBW and LBM were obtained directly. Mean interspecific TBW/LBM ratios were calculated for the three relative age classes adult, sub-adult and juvenile (for species specific age class definitions, see Table 18, Chapter 5). The mean value was then used later in the estimation of fat by the tritiated water technique.

Indirect fat estimation by the tritiated water technique (HTO)

The restrictions in the number of sacrificed animals obtainable in each trapping period made stomach content analysis and body condition assessment virtually impossible to analyse and compare statistically. While nothing could be done about increasing sample size for stomach content analysis, the use of tritiated water represented a non-destructive method of fat estimation, which limited sample size only by logistical capabilites. The tritiated water technique was initiated in the post-drought period, Sessions 5 and 6, for rodents captured in the regular live-trapping programme.

This technique relies on a known amount of the radioactive isotope, HTO, being injected into an animal's body and after a period of time, becoming uniformly dispersed and diluted in the subject's body fluids. After an equilibration period, a body fluid sample, such as blood or urine, is taken. The water portion is extracted by sublimation and the concentration of the isotope is determined in counts per minute (CPM) in a scintillation counter. A comparison of the CPM of a known dilution standard with that of the equilibrated subject sample after correction for background radioactivity of the scintillation fluid (blank) allows the calculation of total body water (TBW) as follows:

$$\text{TBW (ml)} = \frac{\text{standard CPM - blank CPM}}{\text{equilibration CPM - blank CPM}} \times 100$$

(Green & Dunsmore 1978).

This method, however, makes several simplifying assumptions which must be noted as violations of any of these may lead to errors in the calculation of TBW (Holleman _et al._ 1982). These assumptions are:

1. The experimental subject is in a steady state of body composition throughout the experimental period.
2. TBW of the subject is described by a single compartment and isotopic water is distributed rapidly and uniformly throughout this compartment.
3. Isotopic hydrogen is not incorporated into other body constituents and that it is lost only in the form of water.
4. The specific concentration of isotope in water lost from the body is equal to the specific concentration of the TBW.
5. Neither isotopic nor non-labelled water enters the body through the lung or skin surfaces.

In the post-drought period of the present study, up to 10 animals per species per trapping site (i.e. maximum of 20 animals / species / habitat) were temporarily removed from the live-trapping lines. Animals were transported back to camp in their traps, then weighed and injected intra-peritoneally with 0,01 ml of 5 mCi/ml of HTO. They were placed back in their original traps, set outside in the shade and allowed a 2 hour equilibration period. Animals were then reweighed and given their toe-clip number. Blood samples, preferably enough to fill 2 heparinised capillary tubes, were collected either from the clipped toes or from the clipped end of the tail. The animals were then replaced in their traps, returned to the field and released at their point of capture.

During Session 5, each capillary tube was sealed with Cristaseal (Gelmar-Hawksley Ltd., Lancing, Sussex) and stored in a deep freeze. Water was obtained by sublimation after transporting samples back to the laboratory. The purified water samples were then stored in flame sealed glass tubes until preparation for the scintillation counter. However, due to the loss of some Session 5 blood samples while in deep freeze storage, water sublimation during Session 6 was carried out at camp. The flame sealed water samples were then transported back to the laboratory for counting.

From each water sample, two 0,05 ml sub-samples were taken and each was thoroughly mixed with 2 ml of standard scintillation cocktail (Insta-Gel, Packard Instrument Co., Dowthos Grove, Illinois) in scintillation vials. These were then counted in a Beckman LS5800 or a Beckman LS1800 liquid scintillation counter. Similar samples of the standard HTO solution (0,01 ml HTO in 100 ml ordinary tap water) and blank solutions (scintillation fluid only) were also run.

For most animals, four water samples were counted. The mean of the counts for each individual was used in the calculation of the individual's TBW estimate. Estimation of the body fat from TBW uses the assumed constant TBW/LBM ratio, where the LBM is estimated by:

$$\text{LBM (g)} = \text{TBW (ml)} / (\text{TBW/LBM ratio (g/ml)})$$

(Holleman _et al._ 1982).

Body fat was then calculated as:

$$\text{Body fat (g)} = \text{Initial body mass (g)} - \text{LBM (g)}$$

(Holleman _et al._ 1982).

Fat, as a percentage of live body mass was chosen as the simplest basis for the comparison of body condition in the diverse array of small mammal body sizes encountered in this study. A better index for comparison is the body fat/lean dry mass ratio used by Caldwell & Connell (1968) but this was avoided because to obtain lean dry mass from the HTO method required further use of and dependence on the accuracy of specific LBM and TBW estimates (lean dry mass = LBM - TBW), which would have complicated any errors associated with the use of the assumed constants (Holleman & Dieterich 1975).

Although HTO provides a non-destructive method of assessing TBW, it is well known that it overestimates TBW (Nagy & Costa 1980, Holleman et al. 1982). To assess the degree and variability of the overestimation, a validation experiment is recommended where the TBW of the same individuals is calculated using both the HTO and dessication techniques. This experiment was performed in February 1984, two months into the post-drought period. Twelve animals were live-trapped in areas at least 4 km from the study sites and injected with the HTO in the same manner as described previously. After the equilibration period, they were killed using an overdose of anaesthetic chloroform and a blood sample was immediately taken. Sacrificed animals were placed in individual plastic bags, sealed and then frozen and later dessicated in a freeze dryer. Actual TBW was determined for each animal and compared to the TBW estimate obtained by the HTO method. These animals were also subjected to fat extraction and used in the determination of the TBW/LBM ratios.

Unless otherwise stated, t-tests for equal or unequal variances were used for statistical analysis of the results. Arcsine transformations were carried out on all results presented as proportions or percentages to normalise the data before significance testing was undertaken. Statistical significance was accepted at the P<0,05 level.

RESULTS

The snap-trapping programme was conducted throught the waxing and waning of a full moon period, at the beginning of the winter season and after almost 18 months of the drought. Trapping success rates were fairly low but similar in both habitats (Table 28). However, despite similar trapping effort and number of individuals caught in both habitats, species richness was four times greater and species diversity almost three times greater in the ACW than in the MKN. Species diversity in the ACW was significantly higher than in the MKN ($P<0,001$, $t=6,02$, $df=26$, Zar 1984).

Table 28: Percentage trapping success (%TS), number of species (S) and individuals (N) captured and species diversity (H') obtained by snap-trapping in the MKN and ACW landscapes of the KNP during May and June 1983. *= significant difference.

	%TS	S	N	H'
MKN	3,3	2	19	0,65
ACW	4,5	8	20	1,83*

The relative composition of the diets of nine small mammal species snap-trapped during the drought are presented in Table 29. Due to the low species diversity captured in the MKN during the drought, only the diet results from Saccostomus campestris could be compared between habitat types but no significant difference was evident (Mann-Whitney U test). For all the rodent species examined, seeds were the major food item. They generally represented about 60% to 99% of the food ingested. Vegetation intake was uniformly low while insect material varied from 1% to 51% of the rodent diets. The two shrew species showed the expected high ingestion of insect matter with comparatively low intake of seeds and virtually no ingestion of vegetation. A comparison with the results of Kern (1981) shows that most species generally increased their insect useage, slightly reduced seed intake and greatly reduced the ingestion of vegetation during the drought period. A more detailed comparison with Kern's work, however, is tenuous due to the the lack of reported confidence limits around his results, the unavailability of his raw data and the low sample sizes of both studies.

Table 29: Diet composition as shown by the mean percentage (±SE) of insect, green vegetation and seed material in the stomach contents of nine species of small mammal during drought conditions (this study) and high rainfall conditions (Kern 1981) in the KNP. [a] Kern's values averaged for both habitats. [b] *Praomys coucha* results quoted from *P. natalensis* results in A-S landscape (MKN) of Kern (1981). [c] *P. natalensis* results quoted from T-D (Terminalia-Dichrostachys) landscape of Kern (1981). The validity for this approach can be found in Gordon & Watson (1985, see back of thesis).

		Drought				High Rainfall (Kern 1981)^a			
		n	Ins.	Veg.	Seed	n	Ins.	Veg.	Seed
Rodent species									
Saccostomus campestris	MKN	7	36(8)	8(4)	55(8)	9	9	12	79
	ACW	7	26(6)	15(5)	60(7)				
Praomys coucha	MKN	12	29(6)	2(1)	69(5)	10^b	18	3	79
	ACW								
Praomys natalensis	MKN								
	ACW	1	51	0	49	12^c	5	32	63
Tatera leucogaster	MKN								
	ACW	2	21(4)	1(0)	78(4)	4	2	42	56
Steatomys pratensis	MKN								
	ACW	2	1(1)	0	99(1)	11	13	4	83
Lemniscomys griselda	MKN								
	ACW	1	24	3	73	11	2	48	50
Aethomys chrysophilus	MKN								
	ACW	1	12	16	72	11	21	32	47
Shrew species									
Elephantulus brachyrynchus	MKN								
	ACW	4	79(7)	1(0)	20(7)	3	50	30	20
Crocidura hirta	MKN								
	ACW	1	67	0	33	7	40	2	58

Changes in environmental conditions, food availability and physical stress may result in consequential changes in the amount of body fat and hence in small mammal body condition. During the drought, body condition of the rodents in both habitats was consistently low, with fat accounting for less than 5% of the live body mass (Table 30). The one exception was Steatomys pratensis, the fat mouse. Even during the poor environmental conditions of the drought, the fat content of S. pratensis represented 22% of its body weight. Because of the ability of S. pratensis to accumulate large quantities of fat (Smithers 1983) and the unequal representation of the species in the two habitats, their results were excluded from the calculation of the ACW community mean. During the drought, there was no significant difference in the percentage body fat of the rodent communities in the two habitats, however, the ACW shrew community was in significantly better condition than the ACW rodent community (P<0,01, t=3,88, df=7). Moreover, there was no significant difference in the condition of the MKN and ACW S. campestris populations nor any difference between the P. coucha and S. campestris populations in the MKN.

The percentage fat calculated in the post-drought periods (Table 30) were a product of the HTO-TBW estimations. A validation experiment and calculation of the TBW/LBM ratios were performed first so that the TBW estimations could be evaluated and the appropriate TBW/LBM ratio obtained for use in the fat estimations. The following inter-specific TBW/LBM ratios (±SE) were calculated from all dessicated and fat extracted animals according to the relative age classes, adult: 0,717±0,004 (n=35); sub-adult: 0,715±0,009 (n=13); juvenile: 0,699±0,030 (n=13). As there was no significant difference between these values, a mean TBW/LBM ratio of 0,712±0,007 (n=61) was computed for use in the calculations of body fat.

The validation experiment showed that the HTO method consistently overestimated the actual TBW with the mean overestimate (± SE) being 35,8±3,6%. The proportional difference (actual TBW / HTO estimated TBW) between the TBW values obtained for each animal was determined and a mean correction factor of 0,743±0,022 for the HTO-TBW estimates was calculated. Consequently, all TBW estimates were multiplied by 0,743 to obtain a corrected TBW before the calculations of fat and body condition indices were undertaken.

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Table 30: Percentage body fat (%BF) (±SE) of 11 species of small mammal during drought and post-drought conditions in the MKN and ACW landscapes of the KNP. *- excluding Steatomys pratensis from community means.

	Drought May/June				Post-Drought Session 5 (March/April)				Post-Drought Session 6 (July/August)			
	MKN		ACW		MKN		ACW		MKN		ACW	
	%BF	n	%BF	n	%BF	n	%BF	n	%BF	n	%BF	n
Rodent species												
Saccostomus campestris	4,6 (0,5)	8	4,0 (0,9)	7	11,7 (1,7)	15	12,3 (1,5)	15	12,6 (2,9)	2	10,1 (2,2)	5
Praomys coucha	4,3 (0,5)	12	--- --	-	9,3 (1,6)	9	7,7 (0,6)	9	24,7 (1,5)	17	15,5 (1,6)	12
Praomys natalensis	--- --	-	2,5	1	--- --	-	20,9	1	--- --	-	20,6 (2,2)	5
Tatera leucogaster	--- --	-	3,8 (0)	2	10,3 (5,2)	3	7,7 (2,8)	5	10,4 (2,4)	4	11,8 (2,9)	3
Aethomys chrysophilus	--- --	-	2,8	1	--- --	-	3,0 (1,1)	3	--- --	-	18,5 (8,5)	2
Lemniscomys griselda	--- --	-	4,1	1	8,4	1	--- --	-	6,1	1	--- --	-
Steatomys pratensis	--- --	-	22,0 (10,8)	2	--- --	-	--- --	-	--- --	-	--- --	-
Aethomys namaquensis	--- --	-	--- --	-	--- --	-	--- --	-	16,2 (3,3)	5	--- --	-
Graphiurus murinus	--- --	-	--- --	-	--- --	-	13,9 (4,5)	3	--- --	-	--- --	-
Shrew species												
Elephantulus brachyrynchus	--- --	-	6,0 (1,0)	4	--- --	-	--- --	-	--- --	-	--- --	-
Crocidura hirta	--- --	-	12,1 (0,7)	2	--- --	-	--- --	-	--- --	-	--- --	-
Totals												
Rodent comm.	4,4 (0,4)	21	3,8*(0,6)	12	10,6 (1,1)	28	10,1 (1,0)	36	19,8 (1,6)	29	15,2 (1,2)	27
Ex-P. coucha comm.	4,6 (0,5)	8	3,8*(0,6)	12	11,3 (1,5)	19	10,9 (1,3)	27	12,7 (1,8)	12	15,0 (1,8)	15
Shrew comm.	--- --	-	8,0 (1,5)	6	--- ---	-	--- --	-	--- --	-	--- --	-

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Although the condition of both rodent communities had significantly increased between the drought and Session 5 sampling periods (P<0,001, MKN: t=4,30, df=34; ACW: t=3,46, df=45) (Table 30), there was still no significant difference between the two community mean values. Within the MKN community, body condition of the four species was still very similar. Although S. campestris appeared to be in slightly better condition than P. coucha, the difference was not significant. In the ACW community, however, S. campestris was in better condition than P. coucha (P<0,02, t=2,54, df=20). Despite P. coucha and Tatera leucogaster having identical percentage fat values, S. campestris, statistically speaking, was not in better condition than T. leucogaster (P>0,10), however, this was due to the low sample size and high variability in the T. leucogaster values. While there was some intra-habitat variability in the condition of the ACW species, neither the S. campestris nor the P. coucha populations in the ACW were significantly different from their MKN counterparts.

In Session 6, the general body condition in both communities continued to significantly increase despite it being a late post-drought, winter season (MKN: P<0,001, t=4,58, df=54; ACW: P<0,002 t=3,47, df=57) (Table 30). For the first time however, a significant difference between the two community values was evident. The rodent community of the MKN was in significantly better condition than the ACW community (P<0,05, t=2,12, df=53).

The greatest changes in both communities occurred in the Praomys coucha populations (Table 30). The increase in the condition of both P. coucha populations was highly significant (MKN: P<0,001, t=5,65, df=14; ACW: P<0,005, t=3,55, df=16), however, the rate of percentage fat increase for the species in each habitat was quite different. This resulted in the MKN population showing greater amounts of body fat than the ACW population (P<0,001, t=4,21, df=20).

By excluding the differentially successful and numerically dominant P. coucha populations from the community results, the significant difference between the two communities disappears (P>0,20) (Table 30). However, a comparison of the ACW P. coucha population with the rest of the ACW community, hereafter called

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the ex-P. coucha community, showed that they were not significantly different from each other and therefore, the difference between the condition of the rodent communities in the MKN and ACW was due entirely to the large increase in body condition by the MKN P. coucha population. While the general condition of the MKN ex-P. coucha community did not significantly increase from Session 5 to Session 6, the increase in body condition of the ex-P. coucha community in ACW was significant (P<0,05, t=2,25, df=31). However, the extent of the increase in the ACW non-P. coucha community was not as great as that of the P. coucha population (27% cf 50% respectively).

S. campestris did not improve its body condition after Session 5 in either habitat (Table 30). The MKN Session 5 showed no significant difference between the body conditions of S. campestris and P. coucha, however, in Session 6 P. coucha was in significantly better condition (P<0,02, t=2,81, df=17). In the ACW Session 5, S. campestris was in better condition than P. coucha, while there was no difference in Session 6.

DISCUSSION

While the snap-trapping programme was successful in that it produced the necessary small mammal specimens, the trapping success rates were substantially lower than those reported for the live-trapping sessions run just before (Session 2, March/April and after (Session 3 July/August), (see Table 9, Chapter 4) the snap-trapping programme. The MKN showed a 10,4% and 16,7% live-trapping success during Sessions 2 and 3 respectively while in the snap-trapping, it was only 3,3% (Table 28). The ACW showed 7,6% and 7,0% trapping success rates in the live-trapping periods cf only a 4,5% rate in the snap-trapping. The lower snap-trapping success rate could have been influenced by two factors. First, live-trapping success rates could have been artificially high because of the influence of readily available food and "trap-habituated" animals. Numerous recaptures of the same individuals, especially in the low density situations, could raise trapping success. This learned behavior obviously does not have the chance to develop in a snap-trapping programme and therefore would not influence trapping success rate. However, the practise of removing a live-trap for a 24 h period if it captured the same individual on two consecutive nights should have limited this bias to some degree. Secondly, the snap-trapping was unavoidably conducted around a full moon period. Above-ground activity of small mammals is often considerably reduced during high intensity moonlight nights (Gentry, Golley, & McGinnes 1966, Owings & Lockard 1971, Lockard & Owings 1974a, 1974b, O'Farrell 1974). The reduction in activity is suggested to be a behavioural response to reduce predation risk (Clarke 1983, Kotler 1984b). In the drought conditions, grass cover was very low (Chapter 3) and predation risk during the full moon would have been maximal and thus small mammal activity may have been significantly inhibited. This is supported by the noted increases in trapping success in both the snap-trapping and some live-trapping occasions when clouds obscured the moon for greater parts of the night (pers. obs.), a phenomenon which has been noted by numerous other authors (Gentry & Odum 1957, Getz 1961c, O'Farrell 1974).

The higher diversity index and the greater number of species captured in the ACW snap-trapping follows the same trend found in the live-trapping programme. Thus while the number of animals captured in the snap-trapping program was restricted and the trapping success rates were rather different, the specimens collected in each habitat were fairly representative of the relative small mammal community structures at that time.

The diet composition results presented here generally support the diet information reported in the literature (De Graaff1981, Rautenbach 1982, Smithers 1983), that is, the rodents appear to be primarily granivorous with some intake of insect and vegetation and the shrews are primarily insectivores with some intake of seeds but virtually no ingestion of vegetation. The changes in the diet compostion when compared with Kern's (1981) results are not surprising given the dire environmental conditions of the time. Considering the lack of primary production during the drought period, the reduction in vegetation intake by the rodents and shrews may have been due to the availability of only the lignified and nutritionally poor vegetative parts. The decline in seed consumption as well as the increased insect useage by the rodents suggests that seeds may also have been scarcer than normal. Although seeds remain intact and obtainable in the soil seed reserves for varying periods of time after their production, the controlled burn could have significantly reduced their surface availability. Moreover, Nelson & Chew (1977) showed that low soil seed reserves generally occur in the second year of a poor rain period. Although, they suggest that only very high rodent densities could actually reduce the soil seed reserves, Pulliam & Brand (1975) suggest that significant reduction of the seed reserves can occur following a low rainfall year if rodents, birds and ants are all actively foraging. Thus the combination of fire, consumption by all granivores and the general lack of primary production of both the grass and tree communities during the drought undoubtably would have kept the soil seed reserves low.

Other workers in Africa have also found shifts in diet composition as various food sources become scarce. Neal (1984), in Uganda, found that Tatera nigricauda increased insect useage during the drier months while leaf material was maximally ingested during the rains. Field (1975), working in Zambia, found consistent insect useage by Praomys natalensis throughout the year but its importance in the diet increased in the dry season. In contrast to studies showing increased insect useages in the dry season, Field (1975) found increased insects in the diet of Lemniscomys striatus during the wetter months while Perrin (1981) found increased insect and seed intake by Rhabdomys pumilio, primarily a grass eating species, related to Lemniscomys following heavy rainfall periods. My results tentatively suggest greater insect useage by all species during the dry conditions of the drought. It seems likely that this may have occurred due to a shortage of easily digestible green vegetation and possibly a lowered seed supply.

The body condition results obtained during the drought showed that the rodents, at approximately 4% body fat, were in poorer condition than at any other time in the study. Kleiber

(1961) reports that a fat level of 2,5% or less is not available as metabolisable energy and it is indicative of starvation condition. The 3-4% fat levels in my rodents suggests that they were only just surviving, while the shrews with 6 - 12% fat were faring much better. It is possible, however, that the animals snap-trapped in the drought, represented a biased sample. Because the snap-trapping programme was conducted over the full moon period and foraging/ activity during such high risk times is generally reduced (Owings & Lockard 1971, Lockard & Owings 1974a, 1974b, Kotler 1984a), the animals captured may have been those which were forced to forage at these times due to extremely poor body condition. To examine this possibility, a comparison of the mean body mass of each snap-trapped species was made with the means calculated from the live-trap Sessions 2 and 3 (conducted around new moon). Comparisons of the mass means did not reveal any significant differences (S. campestris P>0,50, P. coucha P>0,10, E. brachyrynchus P>0,50) within species over the two intensity moonlight conditions. Thus, the body condition of the snap-trapped animals, as it would relate to body mass, was probably representative of the populations at the time. species, were representative of their populations at the time.

Field (1975) found body fat for rodents to be lowest during the peak breeding season when energetic demands are acknowledged as being extremely high. In my study, while there had been a high percentage of breeding animals in Session 2 ($\bar{x}$ = 74%), by the time of the snap-trapping programme, only 28% of all the animals showed remnants of breeding activity therefore, the energetic demands of breeding could not be solely responsible for the low body condition. If the post-breeding improvement in body condition found by Field (1975) and Caldwell & Connell (1968) was also present in these communities, then body condition during breeding could have been even lower.

Insects have often been shown to be good sources of dietary protein and fat (Field 1975 and references therein), the fact that the shrew community was in significantly better condition than the rodent community implies that insect availability was reasonable. As the rodents in my study were using greater amounts of this food source than it seems they might have under better environmental conditions, perhaps they were less efficient at either capturing or metabolising insects than the shrews. Perrin (1981), studying _Rhabdomys pumilio_, primarily a grass-eater, also found a decrease in fat levels as its insect useage increased.

Following the rains, primary production by the vegetation communities had returned and it is likely that the food/seed supply had increased. If food/seeds had been a limited resource for the rodents during the drought, then the return of good environmental conditions and the greater availability of preferred foods may have resulted in improvements in their body condition. The tritiated water method was initiated in the post-drought period as a non-destructive method for body condition assessment to investigate this possibility.

First however, a short discussion of the HTO methodology is necessary. As stated previously, the fact that TBW is overestimated by HTO is widely accepted and it is recognised that an overestimate of TBW causes an underestimation of the fat mass and body condition. To provide a realistic estimation of fat mass, the overestimation of TBW had to be identified and corrected for. The overestimation of TBW in the present study was fairly large but consistent. It was not within the scope of the present study to identify the specific reasons for the overestimation of TBW, however, Nagy & Costa (1980) and Hollemann _et al._ (1982) discuss in detail the various potential causes for this phenomenon. The low variability in the overestimations suggested that the error was not a random one but a systematic one and therefore a general correction factor could be calculated. The use of a correction constant plus the constant TBW/LBM ratio, however, provides many opportunities for potential error in the fat estimation of individual animals, thus acceptance of an individual's results must be made with caution (Holleman & Dieterich 1975). The use of species and community means should have minimised the effect of such errors. The consistency of the species and community results observed in Session 5 seem to bear this out. However, to avoid unnecessary dependence on actual values, all comparisons of these results were of a relative nature rather than an absolute one.

Field (1975) found a general increase in body fat levels with the cessation of breeding activity, while Caldwell & Connell (1968) found a 2 - 4 fold increase in the fat levels of reproductively active captive animals with ad libitum food. Following the drought, rodent body condition in the present study increased dramatically, however, this could not be attributed to reduced breeding activity as the communities in both habitats showed high percentages of breeding animals (Chapter 5). The improved condition was more likely to have been due to the increased food supply generated by the primary production of the vegetation (Chapter 3). Low rodent densities were present when the drought broke and it is likely that the food supply was being replenished at a faster rate than the rodents could consume it (Nelson & Chew 1977). Body condition of both communities during Session 5 was very similar suggesting there was sufficient food for all species in both habitats to support not only reproduction but also increased fat deposition.

Session 6, however, revealed a different situation. P. coucha in the MKN showed a tremendous increase in body condition while the rest of the species did not. Both Lidicker (1973) and Cole & Batzli (1979) noted that fat levels and density figures often show similar trends and this seems to be reflected in these results as well. In MKN Session 5, the density of all species increased as did their fat levels. In the MKN Session 6, condition of most species did not increase while their density figures declined markedly. P. coucha, on the other hand, showed a tremendous increase in fat as well as density.

It appears then that the MKN habitat had ample space and food for P. coucha to increase both individual and population size. It seems contradictory then that in such a rich habitat the rest of the community (ex-P. coucha community) declined in number and did not improve body condition. Assuming environmental/food conditions had remained stable, Session 6 as a non-breeding season should have resulted in a surge of body fat deposition due to reduced energy demands (Caldwell & Connell 1968). The lack of improvement in the body condition of ex-P. coucha community indicates that environmental conditions may have been either unstable or that food was unequally available to all species. As *P. coucha* increased fat levels so greatly at this time, it is unlikely that food was insufficient thus unequal availability of food seems reasonable.

This food dichotomy could arise from a variety of situations but two seem particularly plausible. First, heterogeneity in the MKN grass layer rapidly reduced after the rains (Chapter 3). The grass layer became extremely uniform and covered a vast expanse of ground. Loss of different microhabitats may have led to possible food and space limitations for the other species (Rosenzweig & Winakur 1969). However, some of the other species, such as *Lemniscomys griselda* and *Crocidura hirta* also prefer uniform grasslands (Smithers 1983) yet they still declined in number.

Secondly, due to the extremely high density of *P. coucha*, the occurrence of direct and/or indirect competitive interactions may have increased to such an extent that all other species were disadvantaged (Thompson 1982, Rebar & Conley 1983). Direct interaction, which implies aggression, seems unlikely as *P. coucha* was one of the smaller species in the community. However, as *P. coucha* density increased, the simultaneous capture of more than one individual in a single trap occurred with increasing frequency, implying that the animals were foraging in groups. Multiple captures of *Praomys* individuals under high density conditions was also noted by Chidumayo (1980). If *P. coucha* individuals did tend to forage in groups it is possible that profitable aggressive interactions against the more solitary species could have resulted. This suggestion, however, is highly speculative as no field evidence of inter-specific aggression was ever obtained.

Indirect interactions between *P. coucha* and the rest of the community suggest reduced food availability due to the high energetic demands of the large *P. coucha* population. Yet if food became scarce enough for the other species to prevent improved fat levels, despite the cessation of breeding, how could the *P. coucha* population obtain sufficient food for its own increase? This suggests that *P. coucha*, besides utilising the food available to all species was perhaps able to obtain an additional food source which was unavailable to the other species. To assess this possibility, however, an extremely detailed dietary composition study would need to be undertaken.

In the ACW, the situation was rather different. Both *P. coucha* and the ex-*P. coucha* community, significantly increased their fat, although *S. campestris* did not. Both increases, that of the *P. coucha* population and the non-*P. coucha* community, however, were much lower than that of *P. coucha* in the MKN. The level of body condition in the ACW community as well as the non-*P. coucha* community in the MKN were only slightly higher than that found by Field (1975) for animals in the non-breeding season. Thus it is possible that the modest increase in condition reflects a decrease in energy demands rather than an increase in energy intake, suggesting that food was not in super abundance. The low non-adult mass gains (Chapter 5) suggests also that the available food may not have been sufficient to support the high nutritional/ energetic demands of rapid body growth by the young animals.

P. coucha in the ACW, as in the MKN, increased density at a higher rate in Session 6 than the other species, however, the fat increases for all the ACW species were much the same. If *P. coucha* was similarly detrimental in some way to the other species as it appears to have been in the MKN, then whatever was controlling the ACW *P. coucha* population was perhaps indirectly allowing the other species to maintain increasing body condition. One obvious difference is the inherent patchiness of the ACW, which may have limited *P. coucha*'s foraging areas. This might allow the other species greater access to some food supplies or just less competition for food in general.

While the densities of the two *P. coucha* populations were very different in Session 5, their fat levels were not, suggesting there was sufficient food for each population. The condition of the two populations by Session 6, however, was very different, indicating that environmental conditions for the *P. coucha* population in the ACW were not as optimal as for the MKN population. The level of *P. coucha* body condition in the MKN was much higher than any reported by Field (1975) or Perrin (1981). This suggests that the MKN *P. coucha* population was responding to more than just the reduced energy requirements of the post-breeding season.

As P. coucha is not a food hoarder, the obvious explanation for the greater fat increase by the MKN P. coucha population is a large surplus or continual replenishment of the food supply. In Chapter 3, it was shown that grass biomass and primary production in the ACW had declined while it was still significantly increasing in the MKN. Although most of the flowering and seeding was over, the continued increase in primary production would result in a certain amount of food supply replenishment. In the ACW, only the grassland patches would have been able to still add to the food supply but these areas were of limited size. A smaller amount of food would have been produced and it would have had a highly concentrated distribution and it seems it was not sufficient to allow the tremendous fat build-up seen in the MKN population.

Besides quantity of food, quality can also affect an animal's energy intake. It is well known that soils derived from sedimentary rock, such as the soil in the ACW, are relatively nutrient poor when compared to soils derived from igneous rock as in the MKN. The analysis of chemical composition of the soils in the two habitats bears this out (Appendix I). While the differing nutritional value of the two soils would probably not affect the nutritional quality of the seeds produced by the same grass species in both habitats, it could influence the amount of seeds produced by specific plants and which species are present. While there was some similarity in the grass species composition of the two habitats, the abundance and distribution of the species were quite different (see Chapter 3, Appendix IIb). Quality of a rodent food source depends not only on energy content but also on abundance and ease of capture and handling times (Brown & Lieberman 1973, Schoener 1974). In this way, it is possible that the quality of available food may have been quite different.

Earlier, it was questioned whether P. coucha in the MKN may have been using an additional food source to allow its tremendous fat increases. The more modest fat increases by the ACW P. coucha suggests that such a food source, if it existed, was not as abundant in the ACW. Because P. coucha is a grassland species, differences in the grass community composition may be particularly relevant. *Bothriochloa radicans* represented 86% of the MKN grass community while it was only 32% of the ACW. Although this grass species is generally considered unpalatable to most animals, its efficient use of this grass would be a distinct advantage, especially as *B. radicans* has both an early and late flowering/seeding period (Gibbs Russell 1983). To test this possibility, however, would require an intensive diet composition, seed nutrition and availability study, a major undertaking in its own right. The idea, however, is appealing because if it proved to be correct, it would explain both the inter- and intra-habitat differences in the body condition.

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CHAPTER EIGHT

GENERAL DISCUSSION

In this study, I have addressed the question of population and community regulation of the small mammal communities living in two different habitats of the Kruger National Park. Each habitat had the same history of burning and due to their proximity to each other, experienced the same climatic events. In the present study there was extreme drought for two years after the triennial burn during which the vegetation communities did not recover, followed by a year of more normal precipitation levels and a return to good veld conditions (Chapters 2 & 3). Monitoring the small mammal populations through these extreme climatic changes allowed the question of regulation to be explored not only in communities in different habitat types but also within habitats under different climatic conditions.

The results of preliminary trapping tests indicated that techniques suited to low population levels should be used to pursue the objectives of the study. For two thirds of the study period, these techniques proved satisfactory but as conditions improved the reliability of the techniques decreased (Chapter 4). Rather than change the methods and because of physical and financial limitations, the techniques were continued but supplementary techniques were used to confirm the results (e.g. density estimation using more than one method (Chapter 4) and body condition assessment using a non-destructive technique (Chapter 7)).

While Appendix V suggests both physical and mathematical techniques for examining various questions in small mammal ecology, the major tactical lesson the present study has emphasised is the need for flexibility. Not only should techniques be assessed continually to make sure they are adequate for obtaining the desired goals under changing conditions but also, the research goals themselves must realistically flex with

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the environmental and small mammal conditions of the time.

To address the second and third objectives of the study, that is to compare community and population dynamics over a two year period and to identify which factors were influential in regulating the communities, four questions are posed.

1) What was limiting each community/ population in the drought and was it the same factor in both habitats and for all species?
2) What were the influential factors in community/ population regulation in the post-drought period and, again, was it the same for all species?
3) What were the similarities and differences in the regulation processes in the communities/ populations under drought and post-drought conditions?
4) How does small mammal community and population regulation evidenced here fit in with the overall management policies of the Kruger National Park, especially that of triennial rotation burning?

Population Regulation

Drought Period

Small mammal numbers were very low (<4 a/ha) during the entire first year of the study, which coincided with the second year of drought conditions (Chapters 2 & 4). Despite an active breeding season, breeding success was poor as no increase in population size was evident. Detailed examination of the population dynamics of *Saccostomus campestris* and *Praomys coucha* revealed that while most of the populations was reproductively active, very few young animals of either species were entering the populations (Chapter 5). The sex ratio of the adult animals was shown to be male-biased in all populations, however, the non-adult sex ratio was 1:1, showing that the adult sex ratios were probably a result of influences after birth rather than an inherently skewed sex ratio at birth. This strongly suggests that mortality among the adult female members of the populations

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was unusually high. Adult female mortality, especially during the breeding season, would directly effect, independently of sex, the number of young animals surviving to enter the trappable population.

It was hypothesised that the increased energetic demands of reproduction would have been difficult to satisfy in the drought-stricken environment, thus leaving the females in poor condition, perhaps unable to support sufficient lactation to ensure survival of the food/milk dependent nestlings. The low percentages of body fat (about 4%) found in animals taken during the drought confirmed the poor condition of the animals (Chapter 7). The fact that body fat was assessed after the breeding season when energetic requirements would have already been reduced to just body maintenance requirements rather than both body maintenance and reproduction suggests that body condition may have been even lower during the breeding season. However, the non-adult mass gains observed between trapping sessions suggested that there was sufficient food available at least to support the nutritional demands of body growth. Both growth and reproduction require additional amounts of energy, however, as growth occurrs over a longer time period than reproduction or at least lactation, then the amount of energy on a daily basis and the urgency with which it is needed is less for growth than for reproduction (Crampton & Lloyd 1959, Hanwell & Peaker 1977). Thus it appears that the food supply in each habitat was sufficient over the long term to support body growth and body maintenance of a few individuals (<4 a/ha) but perhaps was not sufficient for the urgent energetic demands of reproduction.

To meet the increased energetic demands of reproduction, the females would have needed either increased food intake or food quality. It is unlikely that either food quality or quantity improved during the drought, therefore only increased foraging efforts could have met those needs. Increased foraging in the low cover conditions which existed in both habitats during the drought (Chapter 3) would have greatly increased the probability of predation. Thus survival of the nestlings may have been influenced not only by poor physiological condition of the mothers but also by loss of mothers due to predation. Despite the low numbers of animals in the drought, the utilisation densities showed the greatest concentration of animal activity in the highest cover areas available (Chapter 6). Whether this was because of the greater protection from predators or because the concentration of food was higher under the plants (Nelson & Chew 1977) was not determined, nevertheless, it serves to highlight these two factors as being important influences in the regulation of the small mammal populations at the time.

I would suggest then that in the overwhelmingly harsh conditions of the drought, the numbers of small mammals in both habitats were being limited by poor breeding success which was manifested in a density-dependent and extrinsic fashion through the effects of food and possibly predators on the breeding females. Although evidence for this hypothesis was provided by only two of the species, I believe this situation may have been universally applicable to all species because the cost of reproduction would have been high for any female, regardless of species. The shrew species were shown to be in better condition than the rodents during the drought, suggesting that their food supply, at least in the ACW, was not limiting (Chapter 7), however, their numbers were still very low. Two out of the three shrew species captured in the present study prefer dense cover (Meester 1963, Smithers 1983) which was certainly not available during the drought and therefore perhaps predation was a greater limiting factor for the shrew community.

Following the end of the drought, two phases of population growth could be discerned, the early post-drought period when again the communities in both habitats responded similarly and the late post-drought when the community responses diverged.

Early Post-Drought Period

In the early post-drought period all species increased in number (Chapter 4) and body condition (Chapter 7) in both habitats, suggesting that the previously limiting factors were no longer effective. The rates of population increase were most similar at the community level (Chapter 4) while some differences at the population level (Chapter 5) were evident. The rates of increase by the three detailed species were all much higher than the community increases during the drought. However, the rate of increase by P. coucha (4,60/3 months) and P. natalensis (2,20/ 3 months) in the ACW were too high to be accounted for by reproduction alone and it was accepted that the populations were augmented by immigrating animals (Chapter 5).

The early post-drought period could best be characterised by the apparent lack of immediate regulation of my study populations, that is there were no limiting resources and there was no regulation except by the intrinsic reproductive potential of each species. However, the fact that immigration for some of the species was occurring suggests that some form of regulation was operating in areas nearby. The similar recoveries of the two grass communities would have provided ample food, both in terms of quality and quantity, for the support of reproduction and body maintenance by the low numbers of animals present at the end of the drought. In addition, cover had increased greatly so protection from predators was greatly improved (Chapter 3). Also, increases in the size of the resident predator populations would have lagged behind the small mammal increases due to differences in the generation times of the two groups of animals, thus keeping predator pressure low for a time (Andersson & Erhlinge 1977). The two factors then which were probably limiting the populations in the drought were at least temporarily lifted. Under such conditions, unlimited population growth would be expected.

Unlimited population growth, however, cannot continue indefinitely as the populations at some point will have expanded to such an extent that they will again be confronted with a limiting resource (Caughley 1977). This could occur through new limits in the food supply and available cover, and/or increased predator pressure due to reproduction by resident predators or an influx of migratory predators (Andersson & Erhlinge 1977). Population growth will also reduce naturally as such intrinsically controlled factors as the length of the breeding season and the limits of social tolerances are experienced. Therefore a range and variety of factors could be expected to influence the small mammal populations in the late post-drought period.

Late Post-Drought Period

The late post-drought period was during the non-breeding winter season. Without any other complicating factors, a decline in population rates of increase are expected due to the effects of a limited breeding season. Thus intrinsic population regulation was occurring. However, the large differences in final population sizes and the rates of increase (Chapters 4 & 5) show that for some of the populations, other factors besides a limited breeding season were at work.

Both S. campestris populations declined in the late post-drought. Despite the large increase in population size in the early post-drought, the number of non-adults entering the population was still relatively low, suggesting poor breeding success in my populations. However, poor breeding success would not account for the dramatic decline in adult numbers. Cover availability did not seem to be limiting as utilisation densities were very low which suggests that some other factor/s were regulating the population. Food would be a likely possibility if S. campestris food requirements were particularly strict, however, the species is known for its catholic diet (Smithers 1983) and it is difficult to accept direct food limitations especially in the MKN habitat where P. coucha seemed totally unlimited. The high number of transients implied by the utilisation/ preference discrepancy possibly indicated social limits were being neared, however, it is also difficult to accept this as the cause for such a dramatic decline in both populations.

It was evident from the utilisation densities that S. campestris was maximally using those cover conditions which showed the low densities of P. coucha, especially in the MKN. If the trapping sites (M1, M2, A1, A2) are looked at individually, the inverse relationship of P. coucha and S. campestris densities is very striking. The trapping site within each habitat with the highest density of P. coucha generally had the lowest density of S. campestris. Chidumayo (1980) also found an inverse relationship in the densities of Praomys sp. and S. campestris. This might suggest that S. campestris may be avoiding *P. coucha*. Inter-specific aggression within a community has bee shown to influence the densities of particular species (De Long 1966, Lidicker 1966, Batzli 1968, however, it would be unusual for a larger species to avoid a smaller. I would suggest that there might be some indirect influences of high densities of *P. coucha* on *S. campestris*.

S. campestris is a compulsive hoarder (Earl 1980, Smithers 1983, pers. obs.) and may be dependent upon its food hoard in times of stress or poor foraging conditions such as full moon. Also, the species is an extremely slow mover and seems to be easily preyed upon by small carnivores (De Graaff1981). Given these characteristics, some alternative suggestions for the population decline are subsequently mentioned, however, it is believed that much more information on the inter- and intra-specific behaviours of these two species is necessary before any conclusions can be made. First, the possible raiding of *S. campestris* burrows and seed caches by *P. coucha*, especially if they are communally foraging as previously mentioned (Chapter 7, Chidumayo 1980), may indirectly result in food restrictions. This may force increased foraging time and would increase predation risk especially in full moon periods. This suggestion would account for both the decline in numbers and the lack of expected improvement (due to the reduced energy demands of the non-breeding season) in body condition.

Secondly, the high densities of *P. coucha* may attract large numbers of predators which the slow moving *S. campestris* would be particularly vulnerable to as De Graaff (1981) points out. In the late post-drought phase, very high numbers of African wild cat (*Felis lybica*) were noted in the MKN habitat (Hughes pers. comm.), while increased numbers of diurnal birds of prey and snakes were also observed (pers. obs.).

Thirdly, while adult *S. campestris* are larger than *P. coucha*, nestling and juvenile animals are not. Smithers (1983) notes that *P. natalensis*, under high density conditions, can become cannabalistic. I recorded on one occasion the partial consumption of an injured *Mus minutoides* by an adult *P. coucha* which had been captured in the same trap. De Long (1966) showed the low recruitment of *Mus musculus* was due to direct mortality of the young by *Microtus* sp. Thus perhaps not only food stores but also nests may have been raided when the adults were not there to protect them. This, along with the higher predator pressure suggestion would account for the poor breeding success and decline in adult numbers.

Little can be said about the population regulation of *P. natalensis* during the post-drought. By comparison to its sibling species, *P. coucha*, *P. natalensis* was limited by something, however, neither cover nor social limitations seemed likely candidates and doubt was raised about whether the microhabitat variables measured in this study were of real importance to the species. In addition, the apparent lack of adult females may have been important, however, this could also have been differential trappability of the females. instead. The similar age structure of *P. natalensis* in the sixth session to *P. coucha* where low non-adult mass gain implied food limitations, suggests that *P. natalensis* could also have been influenced by low food. While the two species are known to coexist at fairly high densities (Green *et al.* 1978, 1980), the separation of the two species around Satara during the drought suggests some sort of avoidance and possibly inter-specific interference could have been influential in the post-drought as well.

Population regulation for *P. coucha* occurred differently in each habitat. There was little evidence of limited population growth in the MKN by Session 6, other than natural intrinsic control brought about by a limited breeding season (Chapter 5). While high cover was preferred, cover itself was not found to be limiting as equal densities existed in each cover category. Although, further confirmation of this is necessary, as this could also be an artifact of trap saturation. However, the peaking of the utilisation densities around 30 a/ha suggests that either social or food limitations may be important soon. The fact that MKN rodent biomass in the late post-drought (94% *P. coucha*) was still showing a respectable increase despite the community density nearing the estimated maximum stable density suggests that perhaps social rather than food limitations were approaching. By comparison with the MKN population, the ACW *P. coucha* population showed limited growth. However, the utilisation densities were well below the social tolerances shown in the MKN, therefore some other factor appears to have been limiting. The non-adult mass gain was very low in the late post-drought (Chapter 5) and only a slight improvement in body condition, which could easily be accounted for by the reduced energy requirements of the non-breeding season (Chapter 7), suggests that food may have been the, or one of the, limiting factors. Further support for food limitations was the actual decrease in rodent community biomass despite the slight increase in density.

Superficially, the relationship between population regulation during the drought and post-drought periods for each species seem similar. S. campestris showed poor breeding success during both periods. Even the reasons for poor breeding success are rather similar in that increased predation may be important, however, during the drought, the environmental conditions themselves dictated the situation whereas, in the post-drought, the higher densities of P. coucha may have been a major influence. Comparing the population regulation of P. natalensis between climatic periods is difficult due to its lower numbers and seeming lack of consistent microhabitat preferences, however, it was no doubt limited at times in both periods possibly by food or some unknown microhabitat variable. In contrast to the other species, P. coucha seems to have been extrinsically regulated by the environment during the drought regardless of habitat. In the post-drought, extrinsic regulation by the food supply seemed to occur in the ACW while, as far as the present study monitored, P. coucha in the MKN was facing only intrinsic regulation due to the length of the breeding season. However, other forms of regulation, such as extrinsically controlled food or intrinsically controlled social limitations seemed imminent.

Community Regulation

The regulation of small mammal communities occurs in two ways which may or may not be inter-related. First there is the regulation of community size in terms of species diversity or the number of species present in the community. Second is community size in terms of total abundance or biomass of individuals, regardless of species. Both of these aspects rely to some degree on the factors regulating each species. Specific microhabitat requirements may determine whether a species can even exist in a certain habitat, such as was the case with _Aethomys namaquensis_ which was found in the MKN community but not in the ACW community (Chapter 4), while the extent of specific microhabitats may limit the maximum density each species can obtain (Feldhamer 1979, Rebar & Conley 1983, Price & Waser 1984, Spencer & Cameron 1985). In addition, quantitiy and quality of food can limit communities through diversity of food types and total energy available to be consumed, that is what biomass of small mammal can potentially be supported by the available energy in that habitat. Another possible regulating factor in community size could be the effects of one species upon another. Inter-specific interactions can occur directly through aggression (Batzli 1968, Grant 1970) or indirectly through competition for limited resources such as food or microhabitat (Price 1978, Bowers 1986, Cole _et al._ 1986) nevertheless, both could be important in community regulation.

Community diversity was fairly high but erratic in both habitats during the drought due to the low number of individuals of most species (Chapter 4). As the post-drought period progressed, diversity in the MKN decreased due to the dominance of one species while in the ACW, diversity tended to stabilise at a high level (Chapter 4). It was shown that the community diversity results fit well with current theory in that the more complex habitat, the ACW, had the greater diversity and after the rains with increased primary production, a more stable diversity. In addition, the MKN had its greatest diversity when the habitat heterogeneity was at its highest (i.e. during the drought).

Mentis & Rowe-Rowe (1979) showed the greatest diversity and abundance of small mammals in the Natal Drakensberg to occur in the first three years after a burn, while it was generally after one year that both food and cover had increased sufficiently to allow the colonisation of the areas by diurnal and crepuscular species thus increasing the diversity. However, as the vegetation thickened, diversity again declined due to loss of

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species as the original pioneer species (soon after the burn) left the area. In the present study, it was not the number of species present in each community which changed very much over time but the population sizes which affected the community diversity values. While it is generally accepted that increased habitat heterogeneity yields a greater number and variety of microhabitats which can be exploited, in the present study microhabitat in the form of cover, was not found to be limiting for the common species in either habitat. Nevertheless, it is possible that the variation in quality of each microhabitat as a food supplier was limiting. If this is so, then in the food supply of the different patch types in the ACW may have ensured community diversity by limiting the dominance of P. coucha and thereby reducing its influence on the other species.

Community diversity in the drought then was influenced most likely by the food supply. Insect availability may have limited shrew presence in the MKN, while seed supplies may have limited the rodents in both habitats. it limited the density of the various species themselves. The community size, that is biomass, was also regulated probably through the food supply. The rodents present were in poor body condition during the drought, suggesting there was insufficient food. Therefore, community biomass may have been limited by the energy available in the food supply to support a higher community biomass. However, as mentioned before, the combination of low cover and predators could also have been ultimately limiting the community biomasses.

In the post-drought, the number of species present did not change but the density of each species did which greatly influenced the diversity values (Chapter 4). While some of the species densities could have been limited by the loss and gain of microhabitat availability, this did not seem to be the case for the common species (Chapter 7). I would suggest that diversity and biomass in the post-drought was mediated again through the food supply and by the direct or indirect effects of P. coucha on the rest of the community. Thus what affected P. coucha density ultimately affected the community diversity. The actual decrease in the ACW rodent biomass between Sessions 5 and 6 while the MKN still showed a large increase,again suggests food or predators, however, casual observations suggested that the greatest increase in predators occurred in the MKN not in the ACW and food seems the more likely limiting factor.

Food Supply

Throughout the examination of community and population regulation in the present study, the idea that food supply, at least for the rodents, may have been a major regulating factor at one time or another, for one species or another, has been a recurring theme. Unfortunately, this aspect was not directly investigated in this study. However, to at least explore why the food supply might have been limited, I propose a possible model of the food supply in each habitat, based on the vegetation community results (Chapter 3). In this model the vegetation responses to the changing climatic conditions are depicted and the status and composition of the probable food supply in each habitat is hypothesised (Fig. 18).

Under normal circumstances (i.e. usual summer rainfall pattern, see Chapter 2), the grasses would grow and seeds would become available to the rodents starting in November/ December and peaking about January, while few grass seeds would enter the food supply after May (Fig. 18A, solid line). In contrast, tree seeds, which take longer to produce, would only enter the food supply starting around March/ April and peaking in June/ July (Fig. 18A, broken line). Thus two peaks in seed input can be expected, however, due to the greater diversity in tree species and sizes, the tree seed input is probably less restricted in time, therefore the broader plateau in their maximum input.

In the KNP, every third year in August/September, every block in KNP, on a rotating basis, is burned which, depending on the intensity and extent of the fire, would temporarily destroy or reduce the surface soil seed reserves. Generally, the summer rains starting in October would allow the grass and tree communities to recover and still produce seeds. Thus while their would be a temporary shortage of seeds, replenishment could still be expected and the cycle of seed input would be relatively undisturbed, although perhaps slightly delayed. Following the August 1981 burn, however, this cycle was disrupted by the start of the drought, which for two years did not allow the vegetation to recover (Chapter 3). With no seed input because there was no primary production to speak of by either the grasses or trees, the food supply would not have been replenished and so would have remained at the low post-burn level (Fig. 18B). When the normal rainfall pattern returned in November 1983, albiet slightly later than usual, the recovery by the grass community was immediate and its capacity and potential as a food supplier also returned, that is, the return to primary production probably represented an immediate restoration of its annual amount of seed input (Fig. 8.1C). The trees, however, took much longer to recover their primary production than usual, perhaps due to the nutritional strains of the two year drought and the later rains, and thus the start of the availability of their seeds as a food source was delayed until July (Chapter 3, compare Fig. 18A with 18C).

How would this situation have affected the food supply cycles in each habitat? In the grassland dominated MKN, I have already suggested that grass and forb seeds are the primary food source because the tree community was sparse and most of the common trees were relatively immature (Chapter 3). The annual replenishment of the grass and forb seeds then probably represents the basic food cycle (Fig. 18D, grass seeds line (solid) cf combined seed line (dotted)). The food composition and therefore the cycle in the ACW, however, may be quite different. I believe that trees, grasses and forbs have a far more equal role to play in the food supply. The irregular distribution and lower density of the grass plants suggest that they do not provide the same proportion of the food supply that they do in the MKN. Not only are there large areas with sparse grass covering, even in the post-drought period, but the grass or forb seeds produced there would be far more exposed. The trees are numerous and mature enough to produce a substantial seed crop each year. Therefore, the food supply though possibly similar in abundance, although this is not necessarily so, would certainly have a very different composition (Fig. 8.1G, grass (solid) and tree (broken) lines cf combined seed line (dotted)).

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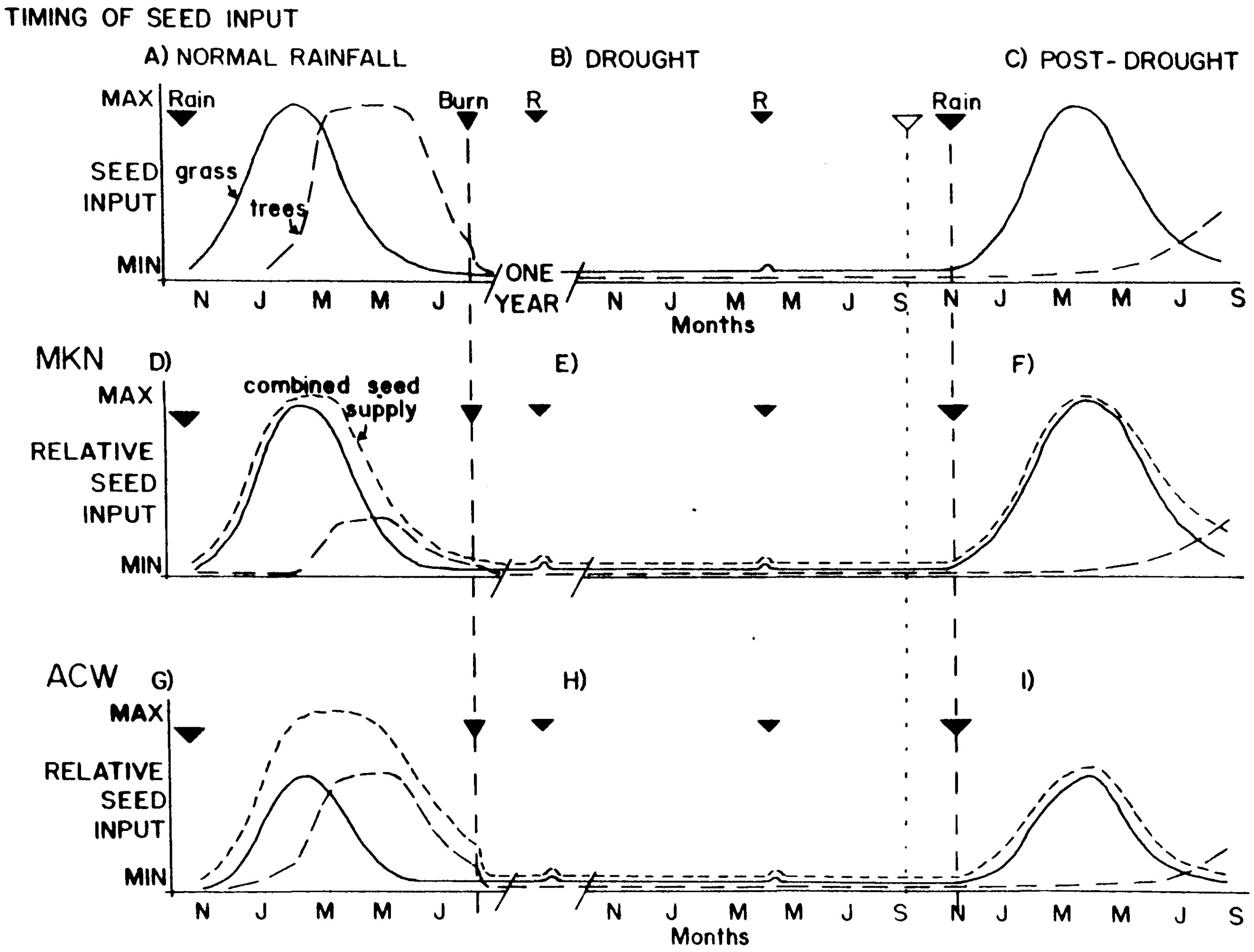
Figure 18: A-C: The seasonality and relative timing of seed fall (minimum input to soil seed reserves July-November, maximum input December-March) by the grass (solid line) and tree (broken line) communities under normal rainfall (A), during two years of drought (B) and in the subsequent post-drought conditions (C) when normal rainfall occurred but was two months later than usual in starting (▽).
D-I: The relative amounts of seed input by the grass and tree communities into the available seed supply (dotted line) in the MKN (D-F) and ACW (G-I) landscapes of the KNP under normal rainfall conditions (D & G respectively), during two years of drought (E & H respectively) and in the subsequent post-drought conditions (F & I respectively).



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The immediate effect of the drought, following after the burn, would have had similar short-term effects on the food supply in each habitat, that is non-replenishment of the soil seed reserves (Fig. 18e, h). The long-term effects, however, were probably very different. The grass communities in both habitats responded similarly to the returning rains in that they were both able to fully recover to their previous potential as food sources, however, the delayed tree community recovery would not really affect the MKN seed supply while it drastically affects the food supply in the ACW (Fig. 18f cf. d & 18i cf. g).

The magnitude of the impact this would have on the recovery of the food supply cycle in each habitat would be quite different. In the MKN, where the grasses were the dominant feature and grass seeds probably the primary food source, the rains would have allowed a quick restoration of the habitat's total food supply, thus rapidly returning the habitat's small mammal carrying capacity to its full potential (Fig. 18D cf. F, dotted line). In the ACW, the rains would allow the same rapid replenishment of the grass and forb seeds but because they represent a smaller proportion of the potential food supply, this would represent only a partial recovery of the food supply and cycle (Fig. 18G cf. I, dotted line). Thus, a residual effect of the drought on the ACW small mammal carrying capacity would remain until the tree seed crop became available. The ACW then may only return to its full carrying capacity potential in stages and over a longer period of time.

According to this model then, food limitations could have occurred and been unusually influential in the small mammal populations during the drought in both habitats and in the late post-drought period of the ACW. The results obtained in the present study support the predictions of this model very well. Low numbers of animals (Chapter 4) and poor body condition (Chapter 7) were observed during the drought, while the ACW populations showed greater limitations in individual and population growth than the MKN populations (Chapters 4, 5 & 7). In addition, when food was hypothesised to have returned to higher levels (the initial flush of seeds produced by the grass community), unlimited population growth and large improvements

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in body condition were observed.

Due to the grass community composition (Bothriochloa radicans, early and late flowering periods, Gibbs Russell 1983) and the larger grass component in the MKN vegetation community, the food supply in the MKN late post-drought would have continued to be replenished and thus was able to support higher densities of small mammals. Both rodent numbers and biomass continued to increase in the MKN in the late post-drought period (Chapter 4). In the ACW, the predicted partial recovery of the food supply suggests a lower than usual carrying capacity of this habitat. If the community was near the habitat's maximum supportable density under those conditions then food limitations could again be evident. Based on the density results, the ACW community at 14,6 a/ha was virtually at the habitat's carrying capacity which was estimated at 14,9 a/ha (Chapter 4). This is further supported by the actual decrease in the ACW rodent biomass from the early to the late post-drought period. Evidence for individual food limitations was also shown by the non-adult mass gains (<2,0 g / 3 months, Chapter 5) and the slight improvement in body condition which was probably due to a reduction in energy demands rather than increased energy/ food intake (Chapter 7).

KNP Management Policies and Small Mammal Community Regulation

In reviewing how both the communities and populations seem to have been regulated in the drought and post-drought periods, it has become evident that regulation occurred in a variety of ways but often through the effects of food supply. The question remains as to how the KNP's overall management practises, especially that of the triennial rotation burning, influence small mammal regulation. First of all, the triennial burn is a density-independent, extrinsic factor. As Kern (1981) pointed out, the burns probably maintain small mammal community diversity over time by altering the habitat conditions and relieving the veld of moribund vegetation. However, this may be an important mechanism only in some habitats, such as the MKN where one vegetation feature is dominant. Species diversity in the ACW would probably be maintained anyway, due to the inherent patchiness (patch type and quality) of the habitat. This non-equilibrium state of the small mammal communities is important in the maintenance of fugitive species, species which are rare, pioneer types or competitively inferior (Blaustein 1981), such as S. campestris may be when there are high densities of P. coucha.

In terms of population regulation, the burning operates in a density-independent manner and probably allows such extrinsic factors as food supply, cover and predator pressure to have increased influence as habitat structure and quality is altered. It was only the coincidence of the drought following the burns which prolonged the initial influence of these factors. However, for the same reason, the drought probably reduced the influence these factors would have had at the higher density levels. Thus, under more normal conditions, these factors may become influential earlier in the three year burn interval than I recorded them, that is in the second year after burn rather than only in the third year.

The present study has suggested how both the communities and populations of small mammals were regulated, however, the drought conditions experienced here could not be considered as a normal situation, although Tyson (1986) and Gertenbach (1980) do highlight the regularity of the dry and wet 10 year weather cycles. Ideally, this same study should be repeated in a period of normal or above average rainfall to compare population regulation under these conditions. Furthermore, this study has highlighted many areas which could benefit from additional research. Such projects could include a more detailed examination of the food preferences of the various species, the quality and quantity of food or even of particular food items such as Bothriochloa radicans in different habitats. A very important study would be the affect of burning on the food supply, especially on the individual components of the food supply and the soil seed reserves themselves and to what extent are the insects, as a food source affected. Additionally, the influence of both migratory and resident predators on the small mammals in different cover conditions and the exact role of cover, that is, is it protection from predators or environmental conditions. Also, how do inter-specific interactions between various species, particularly the influence of varying densities of P. coucha influence community composition? Basic small mammal community composition in the other landscapes of the KNP and what factors influence these communities must also be examined. While the present study has served to answer some questions about the role of small mammals and their regulation in the KNP, it has also raised far more questions than it answered. Further studies are urgently needed to assess, define and explain the importance of small mammals in the flow of energy through the different landscape types and indeed through the entire Kruger National Park ecosystem.

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SUMMARY

1. The small mammal and vegetation communities in the MKN and ACW landscapes of the KNP were monitored for two years following one year of post-burn 'recovery'.

2. Both landscapes were burned in August 1981, however, the subsequent two year drought allowed only limited post-burn recovery of the vegetation.

3. The MKN was a low diversity grassland habitat with few mature trees. The ACW was a complex, high diversity habitat with distinct grassland, woodland and open vlei patches.

4. Habitat heterogeneity increased in the MKN as the drought progressed and decreased with post-drought conditions. Heterogeneity in the ACW was stable and high in both climatic periods.

5. Grass biomass and cover were similarly low in both habitats during the drought and increased at similar high rates in early post-drought but, in the late post-drought, biomass and cover continued to increase in the MKN but decreased in the ACW.

6. Small mammal community diversity in the MKN was high during the drought but decreased markedly in the post-drought as the numerical dominance of *Praomys coucha* increased. Diversity in the ACW community remained high in both climatic periods.

7. Rodent density and biomass were equally low (<4a/ha, <100g/ha) in both habitats during the drought and increased at similar high rates in the early post-drought, however, late post-drought differences were apparent. Density and biomass continued to increase in the MKN to a high of 35a/ha and 950g/ha while density in the ACW remained around 14a/ha and biomass decreased to 400g/ha.

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8. Population dynamics of *Saccostomus campestris* and *P. coucha* were similar in both habitats during the drought showing low density, breeding success and juvenile recruitment, despite high breeding activity. Male biased sex ratios in the adult animals only suggested high adult female mortality.

9. In early post-drought conditions, *S. campestris*, *P. coucha* and *Praomys natalensis* increased density through increased breeding success and immigration.

10. In the late post-drought conditions, *P. coucha* density increased at a greater rate in the MKN than in the ACW. *S. campestris* density decreased in both habitats but more so in the MKN than in the ACW. *P. natalensis* increased density at a slower rate than *P. coucha* in the ACW and was recorded for the first time in the MKN despite a high density at Satara restcamp 5 km away.

11. Grass cover was the most important microhabitat variable in both habitats and both climatic periods, however, cover availability alone could not explain the community and population dynamics.

12. Body condition, as measured by percentage body fat, was low for all species during the drought (<5% rodents, 8% shrews) and increased significantly and similarly in the early post-drought to 10 - 11% body fat. In the late post-drought, *P. coucha* increased to 20% body fat in the MKN but only 15% in the ACW. The other species increased to 13% in the MKN but 15% in the ACW.

13. The small mammal communities in both habitats during the drought were extrinsically regulated by food and predators through their effects on female and non-adult survival.

14. There were no factors limiting population growth during the early post-drought.

15. Population regulation in the two habitats occurred differently within and between species in the late post-drought period. In the ACW it was suggested that all three species were extrinsically regulated again by food. Within the period of this study, *P. coucha* in the MKN was intrinsically regulated by the length of the breeding season, however, social limitations may have been imminent. *S. campestris* may have been influenced again by food and predators, however, this may have been a consequence of high densities of *P. coucha* rather than poor environmental conditions.

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OPSOMMING

1. Die kleinsoogdier- en plantgemeenskappe in die MKN en ACW landskappe van die KNP was vir twee jaar na een jaar van na-branding 'herstelling' nagevolg.

2. Beide landskappe was in Augustus 1981 gebrand, alhoewel die volgende twee-jaar droogte slegs beperkte na-branding herstel van die plantegroei toegelaat het.

3. Die MNK was 'n grasveld habitat van lae diversiteit met enkele volwasse bome. Die ACW was 'n ingewikkelde habitat van hoë diversiteit met duidelike grasveld, boomryk en oop vlei-kolle.

4. Habitat heterogeniteit het in die MKN toegeneem soos die droogte gevorder het, en het afgeneem met na-droogte toestande. Heterogeniteit in die ACW was konstant en hoog in beide klimaatstydperke.

5. Die biomassa en dekking van gras was soortgelyk en laag in beide habitatte gedurende die droogte en het teen soortgelyke hoë tempo's in die vroeë na-droogte toegeneem, maar in die laat na-droogte het beide aangehou toeneem in die MKN maar afgeneem in die ACW.

6. Kleinsoogdier-gemeenskappe se diversiteit in die MKN was hoog gedurende die droogte, maar het merkbaar afgeneem in die na-droogte soos die dominansie in getalsterkte van *Praomys coucha* toegeneem het. Diversiteit in die ACW gemeenskap het hoog in beide klimaatsperiodes gebly.

7. Knaagdier digtheid en biomassa was ewe laag (< 4d/he, <100/ha) in beide habitatte gedurende die droogte, en het teen soortgelyke hoë tempo's in die vroeë na-droogte toegeneem. Aan die ander kant was laat na-droogte verskille duidelik. Digtheid en biomassa het voortdurend toegeneem in die MKN tot 'n hoogtepunt van 35d/he en 950g/he terwyl digtheid in die ACW om en by 14d/he gebly het, en biomassa tot 400g/he afgeneem het.

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8. Bevolkingsdinamika van Saccostomus campestris en P. coucha was soortgelyk in beide habitatte gedurende die droogte en het lae digtheid, voortplantingsukses en jongeling-werwing vertoon, ten spyte van telings=aktiwiteite. Geslagsverhoudings in volwassenes ten gunste van mannetjies het slegs hoë sterftesyfers van wyfies voorgestel.

9. Gedurende vroeë na-droogte toestande hat S. campestris, P. coucha en Praomys natalensis toenemende digtheid deur 'n toename in voort=plantingsukses en immigrasie getoon.

10. Gedurende laat na-droogte toestande het die digtheid van P. coucha teen 'n sneller tempo in die MKN as in die ACW toegeneem. Digtheid van S. campestris het in beide habitatte afgeneem, maar meer in die MKN dan in die ACW. P. natalensis het 'n laer tempo van toename in digtheid dan P. coucha in die ACW getoon, en was vir die eerste keer in die MKN aangeteken ten spyte van 'n hoë digtheid by die Satara ruskamp 5 km daarvandaan.

11. Grasdekking was die mees belangrike mikrohabitat veranderlike in beide habitatte en klimaatstydperke. Dekkingbeskikbaarheid alleen kon egter nie die gemeenskap- en bevolkingsdinamika verklaar nie.

12. Liggaamskondisie, soos gemeet aan persentasie liggaamsvet, was laag vir alle spesies gedurende die droogte (<5% knaagdiere, 8% skeerbekke) en het betekenisvol en ooreenstemmend in die na-droogte tot 10 - 11% liggaamsvet toegeneem. In die laat na-droogte het P. coucha se liggaams=vet tot 20% in die MKN, maar slegs tot 15% in die ACW toegeneem. Die ander spesies het tot 13% in die MKN, maar tot 15% in die ACW toegeneem.

13. Die kleinsoogdier-gemeenskappe in beide habitatte was ekstern deur voedsel en roofdiere gedurende die droogte gereguleer, deur hul uitwerkings op die oorlewing van wyfies en onvolwassenes.

14. Daar was geen faktore wat bevolkingsgroei gedurende die vroeë na-droogte gereguleer het nie.

15. Bevolkingsregulering in die twee habitatte het verskillend binne en tussen spesies in die laat na-droogte tydperk plaasgevind. In die ACW

is dit voorgestel dat al drie spesies weer eens ekstern deur voedsel gereguleer is. Binne die tydperk van die huidige studie was *P. coucha* intrinsiek deur die lengte van die teelseisoen gereguleer alhoewel sosiale beperkinge moontlik binnekort sou optree. *S. campestris* mag moontlik weer eens deur voedsel en roofdiere beinvloed wees, alhoewel dit die gevolg van hoë dighthede in *P. coucha* eerder as swak omgewings= toestande kan wees.

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Appendix I: Chemical composition of the soils in the MKN and ACW landscapes of the KNP. All values are mean of four samples. LOI is loss on ignition, correlating to the carbon content.

Compounds	MKN (wt.%)	ACW (wt.%)
SiO_2	51,83	78,39
TiO_2	4,73	0,78
Al_2O_3	12,31	8,19
Fe_2O_3	11,86	2,70
MnO	0,17	0,04
MgO	1,32	0,42
CaO	2,89	0,33
Na_2O	0,76	0,38
K_2O	1,86	1,91
P_2O_5	0,30	0,08
LOI	11,71	6,49

Trace Elements	ppm	ppm
Co	56,0	14,3
V	221,8	58,0
Cr	236,8	228,0
Cu	116,0	29,8
Ni	120,3	40,3
Zn	91,3	31,3
Rb	46,5	60,3
Sr	621,3	80,8
Y	29,0	14,8
Zr	415,0	210,0
Nb	32,3	11,0

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Appendix II: Tree (A) and grass (B) species composition in the four trapping areas in the MKN (M1, M2) and ACW (A1, A2) landscapes of the KNP. N_I - number of individuals, %C - percentage of the community, %T - percentage of traps having that species. SP75 - least number of species needed to account for 75% of the individuals. Shannon's H' and J' are diversity and evenness indices (see Chapter 3 for details).

	M1			M2			A1			A2		
A. Tree Community	NI	%C	%T	NI	%C	%T	NI	%C	%T	NI	%C	%T
Dichrostachys cinerea	510	35	69	336	28	70	171	11	60	182	11	46
Acacia nigrescens	455	31	91	151	13	72	99	6	40	49	3	26
Grewia bicolor	30	2	27	83	7	50	204	13	60	248	15	76
Erhetia rigida	52	4	37	38	3	13	177	12	26	134	8	24
Euclea divinorum	1	<1	1	8	1	6	29	2	18	332	20	52
Acacia welwitschii	0	0	0	0	0	0	93	6	31	226	14	67
Combretum apiculatum	61	4	34	58	5	41	71	5	13	40	2	11
Ormocarpum trichocarpum	55	4	14	46	4	10	83	5	17	15	<1	7
Acacia exuvialis	76	5	28	98	8	38	16	1	11	6	<1	4
Albizia harveyii	19	1	10	31	3	10	92	6	37	31	2	19
Maerua parvifolia	1	<1	1	1	<1	1	69	5	17	47	3	21
Ziziphus mucronata	3	<1	3	66	6	41	23	1	13	3	<1	3
Combretum imberbe	46	3	34	18	2	19	27	2	20	3	<1	3
Combretum hereroense	24	2	18	27	2	18	19	1	13	2	<1	2
Lannea stuhlmanii	1	<1	1	15	1	2	14	<1	12	37	2	17
Combretum mossambicense	3	<1	3	2	<1	1	55	4	14	0	0	0
Zanthoxylum humilis	0	0	0	0	0	0	12	<1	9	46	3	34
Spirostachys africana	1	<1	1	0	0	0	1	<1	1	53	3	29
Sclerocarya caffra	14	1	13	33	3	24	6	<1	7	1	<1	1
Cissus cornifolia	2	<1	2	5	<1	6	13	<1	10	25	2	20
Commiphora africana	0	0	0	4	<1	2	14	<1	6	18	1	8
Terminalia prunoides	3	<1	3	11	1	9	0	0	0	17	1	7
Lonchocarpus capassa	2	<1	2	7	1	3	18	1	12	2	<1	2
Ximenia caffra	16	1	11	2	<1	2	10	<1	9	1	<1	1
Peltophorum africanum	0	0	0	6	1	6	13	<1	9	8	<1	9
Acacia tortilis	14	1	12	11	1	8	1	<1	1	1	<1	1
Grewia flavescens	0	0	0	7	1	6	15	<1	11	3	<1	3
Grewia villosa	0	0	0	0	0	0	10	<1	9	14	<1	10
Maytenus senegalensis	1	<1	1	2	<1	2	17	1	6	4	<1	3
Cassia petersiana	0	0	0	0	0	0	23	1	6	0	0	0
Commiphora pyracanthoides	0	0	0	4	<1	3	5	<1	2	13	<1	13
Acacia grandicornuta	0	0	0	0	0	0	16	1	6	0	0	0
Grewia monticola	12	<1	12	3	<1	3	0	0	0	0	0	0
Capparis tomentosa	0	0	0	0	0	0	11	<1	2	4	<1	3
Rhus dentata	5	<1	4	1	<1	1	9	<1	3	0	0	0
Pappea capensis	0	0	0	0	0	0	0	0	0	13	<1	12
Maytenus heterophylla	0	0	0	0	0	0	1	<1	1	12	<1	13
Rhigozum zambesiacum	0	0	0	0	0	0	0	0	0	12	<1	8
Ximenia americana	0	0	0	0	0	0	2	<1	1	9	<1	4
Euphorbia tirucalli	0	0	0	0	0	0	0	0	0	10	<1	10
Commiphora neglecta	0	0	0	4	<1	2	1	<1	1	4	<1	3
Albizia anthelmintica	0	0	0	0	0	0	0	0	0	7	<1	8

continued overleaf . . .

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	M1			M2			A1			A2		
	NI	%C	%T	NI	%C	%T	NI	%C	%T	NI	%C	%T
Bolosanthus speciosus	0	0	0	0	0	0	7	<1	6	0	0	0
Grewia hexamita	0	0	0	3	<1	3	2	<1	1	2	<1	2
Rhus guenzi	2	<1	1	5	<1	2	0	0	0	0	0	0
Erhetia amoena	0	0	0	0	0	0	6	<1	1	0	0	0
Carissa bispinosa	0	0	0	0	0	0	0	0	0	6	<1	6
Manilkara mochisia	1	<1	1	0	0	0	2	<1	2	2	<1	2
Acacia nilotica	3	<1	2	1	<1	1	1	<1	1	0	0	0
Ozoroa paniculosa	3	<1	2	2	<1	2	0	0	0	0	0	0
Teclea pillosa	0	0	0	0	0	0	1	<1	1	3	<1	2
Boscia mossambicensis	0	0	0	0	0	0	1	<1	1	2	<1	2
Dinocanthium histerix	0	0	0	0	0	0	0	0	0	3	<1	3
Cordia ovalis	0	0	0	0	0	0	3	<1	3	0	0	0
Acacia erubescens	0	0	0	0	0	0	2	<1	2	1	<1	1
Gardenia spatufolia	0	0	0	2	<1	1	0	0	0	1	<1	1
Commiphora sp.	0	0	0	0	0	0	3	<1	3	0	0	0
Boscia sp.	0	0	0	0	0	0	1	<1	1	1	<1	1
Cassine transvaalensis	0	0	0	0	0	0	1	<1	1	0	0	0
Diospyros mespiliformis	1	<1	1	0	0	0	0	0	0	0	0	0
Cassia abbreviata	0	0	0	1	<1	1	0	0	0	0	0	0
Grewia sp.	0	0	0	0	0	0	0	0	0	1	<1	1
TOTALS												
No. species		32			37			50			49	
No. individuals		1477			1185			1545			1672	
SP75		4			7			11			15	
Shannon's H'		2,03			2,58			3,09			2,74	
Shannon's J'		0,58			0,71			0,79			0,70	

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B. Grass Community	M1		M2		A1		A2	
	%C	%T	%C	%T	%C	%T	%C	%T
Bothriochloa radicans	68	100	80	100	24	74	36	76
Panicum sp.	21	84	7	47	20	83	22	99
Themeda triandra	2	16	8	53	12	59	8	40
Eragrostis superba	7	46	<1	7	4	34	3	26
Cymbopogon excavatus	0	0	0	0	12	60	5	27
Chloris roxburghiana	0	0	0	0	5	27	9	45
Enteropogon monostachys	0	0	0	0	1	8	10	34
Heteropogon contortus	0	0	<1	1	1	16	1	7
Digitaria eriantha	<1	8	<1	1	2	18	1	14
Aristada congesta	1	9	1	16	1	12	1	11
Urochloa mossambicensis	<1	2	<1	3	3	20	1	15
Cenchrus ciliaris	<1	1	<1	2	<1	10	<1	1
Enneapogon cenchroides	<1	5	<1	7	1	11	1	5
Setaria nigrirostris	<1	1	<1	1	<1	1	0	0
Tragus berteronianus	<1	4	<1	3	<1	1	0	0
Sorghum versicolor	<1	3	0	0	0	0	0	0
Sporobolus nitens	0	0	<1	1	1	11	3	24
Rhynchelytrum repens	0	0	0	0	0	0	<1	3
Trichoneura grandiglumis	0	0	0	0	<1	1	<1	1
Tricholaena monachne	0	0	0	0	<1	2	<1	1
Diheteropogon amplectens	0	0	0	0	<1	2	<1	3
Eragrostis gummiflua	0	0	0	0	<1	1	<1	1
Sporobols smutsii	0	0	0	0	2	6	<1	1
Eragrostis cylindriflora	0	0	0	0	2	16	<1	4
Dactyloctenium sp.	0	0	0	0	<1	2	<1	7
Pogonarthria squarrosa	0	0	0	0	0	0	<1	1
Chloris virgata	0	0	0	0	<1	3	0	0
Eragrostis cilianensis	0	0	0	0	<1	3	0	0
Unknown sp. A	0	0	0	0	3	25	4	33
TOTALS								
No. species	12		13		26		24	
SP75	2		1		6		4	
Shannon's H'	1,02		0,78		2,31		2,14	
Shannon's J'	0,41		0,30		0,71		0,67	

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Appendix III: Microhabitat availability (Av) (number of trap nights variable was available) in the environment and frequency of species occurrence with each microhabitat variable in the MKN and ACW landscapes of the KNP in drought and post-drought conditions. Microhabitat variable abbreviations as in text, Table 24, Chapter 6. Sc-*Saccostomus campestris*, Pc-*Praomys coucha*, Pn-*Praomys natalensis*, Tl-*Tatera leucogaster*, Ac-*Aethomys chrysophilus*, An-*Aethomys namaquensis*, Sp-*Steatomys pratensis*, Lg-*Lemniscomys griselda*, Ch-*Crocidura hirta*.

MKN DROUGHT

VARIABLE & CATEGORY			Av	Sc	Pc	Pn	Tl	Ac	An	Sp	Lg	Ch
GSD	L	<0,33	3573	208	161	--	3	--	0	4	4	--
	M	0,34-0,66	2091	81	53	--	1	--	19	0	5	--
	H	>0,66	31	0	1	--	0	--	0	0	0	--
VGH	L	<33	1392	56	37	--	0	--	0	2	3	--
	M	34-66%	4034	213	169	--	3	--	10	4	4	--
	H	>66%	225	16	14	--	1	--	0	1	2	--
%GC	L	<33%	4754	212	164	--	2	--	6	3	6	--
	M	34-66%	856	73	56	--	2	--	0	1	3	--
	H	>66%	0	0	0	--	0	--	0	0	0	--
TSD	L	<0,33	797	25	16	--	0	--	0	0	0	--
	M	0,34-0,66	3103	166	116	--	2	--	6	3	7	--
	H	>0,66	1795	98	83	--	2	--	13	1	2	--
TD0,5	L	0-5	3107	186	127	--	3	--	6	1	6	--
	M	6-10	1334	56	36	--	0	--	13	1	0	--
	H	>10	1254	47	52	--	1	--	0	2	3	--
TD1	L	0-4	3198	164	132	--	3	--	6	2	4	--
	M	5-10	1819	86	68	--	0	--	13	2	0	--
	H	>10	678	39	15	--	1	--	0	0	5	--
TD4	L	0-4	4850	257	194	--	4	--	13	4	5	--
	M	5-8	543	17	12	--	0	--	6	0	1	--
	H	>8	302	15	9	--	0	--	0	0	3	--
TD>4	L	0-2	5605	287	214	--	4	--	19	4	9	--
	M	3-5	90	2	1	--	0	--	0	0	0	--
	H	>5	0	0	0	--	0	--	0	0	0	--
ROC	L	0&1	5339	269	215	--	4	--	0	4	9	--
	M	2&3	203	12	0	--	0	--	0	0	0	--
	H	4&5	153	8	0	--	0	--	19	0	0	--
LIT	L	0&1	4541	247	195	--	3	--	0	2	9	--
	M	2&3	920	40	18	--	0	--	6	2	0	--
	H	4&5	234	2	2	--	1	--	13	0	0	--
FOR	L	0&1	2188	162	103	--	0	--	6	2	1	--
	M	2&3	2732	102	93	--	3	--	13	2	5	--
	H	4&5	775	25	19	--	1	--	0	0	3	--

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MKN RAIN

VARIABLE & CATEGORY			Av	Sc	Pc	Pn	Tl	Ac	An	Sp	Lg	Ch
	L	<0,33	1430	148	640	8	11	--	0	--	8	9
GSD	M	0,34-0,66	871	106	326	3	17	--	22	--	6	2
	H	>0,66	13	4	4	0	0	--	0	--	0	0
	L	<33	261	18	155	2	4	--	0	--	5	8
VGH	M	34-66%	1914	224	876	8	13	--	12	--	9	3
	H	>66%	113	15	67	1	6	--	0	--	?	0
	L	<33%	193	41	36	0	7	--	0	--	0	0
%GC	M	34-66%	1471	197	598	5	15	--	12	--	9	5
	H	>66%	628	19	464	6	6	--	0	--	5	6
	L	<0,33	301	31	120	3	2	--	6	--	0	2
TSD	M	0,34-0,66	1287	145	532	6	19	--	9	--	12	5
	H	>0,66	729	82	318	2	7	--	7	--	2	4
	L	0-5	1226	106	521	9	8	--	9	--	3	6
TD0,5	M	6-10	563	79	224	2	6	--	7	--	4	4
	H	>10	525	73	225	0	14	--	6	--	7	1
	L	0-4	1263	139	523	9	17	--	9	--	4	5
TD1	M	5-10	773	95	338	0	5	--	13	--	4	5
	H	>10	278	24	109	2	6	--	0	--	6	1
	L	0-4	1983	214	840	11	21	--	13	--	14	10
TD4	M	5-8	219	31	85	0	7	--	9	--	0	0
	H	>8	112	13	45	0	0	--	0	--	0	0
	L	0-2	2287	256	955	11	28	--	22	--	14	11
TD>4	M	3-5	27	2	15	0	0	--	0	--	0	0
	H	>5	0	0	0	0	0	--	0	--	0	0
	L	0&1	2226	254	961	11	28	--	1	--	14	11
ROC	M	2&3	43	4	8	0	0	--	5	--	0	0
	H	4&5	45	0	1	0	0	--	16	--	0	0
	L	0&1	1862	206	802	9	24	--	6	--	5	7
LIT	M	2&3	355	45	142	2	3	--	10	--	9	4
	H	4&5	97	7	26	0	1	--	6	--	0	0
	L	0&1	859	103	379	6	4	--	5	--	5	7
FOR	M	2&3	1140	127	458	5	13	--	12	--	9	3
	H	4&5	315	28	133	0	11	--	5	--	0	1

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ACW DROUGHT

VARIABLE & CATEGORY			Av	Sc	Pc	Pn	Tl	Ac	An	Sp	Lg	Ch
	L	<0,33	175	17	0	0	1	4	--	1	0	0
GSD	M	0,34-0,66	3701	206	3	6	13	11	--	6	5	6
	H	>0,66	2127	95	1	17	7	8	--	5	0	1
	L	<33	644	31	0	2	1	0	--	0	0	3
VGH	M	34-66%	4414	238	3	8	12	20	--	8	5	4
	H	>66%	928	52	1	13	11	3	--	4	0	?
	L	<33%	4932	264	0	2	11	7	--	8	0	0
%GC	M	34-66%	1009	56	4	8	10	16	--	4	5	6
	H	>66%	0	1	0	13	0	0	--	0	0	1
	L	<0,33	340	21	2	2	4	0	--	1	0	0
TSD	M	0,34-0,66	2837	135	2	11	7	3	--	7	5	2
	H	>0,66	2826	162	0	10	10	20	--	4	0	5
	L	0-5	3551	172	3	9	8	7	--	5	0	3
TD0,5	M	6-10	1065	63	0	1	7	11	--	6	0	2
	H	>10	1387	83	1	13	6	5	--	1	5	2
	L	0-4	4032	216	2	18	16	13	--	12	5	4
TD1	M	5-10	1597	86	2	4	5	10	--	0	0	2
	H	>10	374	16	0	1	0	0	--	0	0	1
	L	0-4	2590	144	3	13	9	11	--	11	0	4
TD4	M	5-8	1496	67	1	3	7	10	--	0	0	2
	H	>8	1917	107	0	7	5	2	--	1	5	1
	L	0-2	4743	267	4	19	21	20	--	12	5	7
TD>4	M	3-5	1034	41	0	3	0	2	--	0	0	0
	H	>5	226	10	0	1	0	1	--	0	0	0
	L	0&1	6003	318	4	23	21	23	--	12	5	7
ROC	M	2&3	0	0	0	0	0	0	--	0	0	0
	H	4&5	0	0	0	0	0	0	--	0	0	
	L	0&1	3671	207	2	17	17	13	--	10	5	5
LIT	M	2&3	2199	106	2	6	4	10	--	2	0	2
	H	4&5	133	5	0	0	0	0	--	0	0	0
	L	0&1	2421	157	2	8	9	7	--	1	5	7
FOR	M	2&3	3057	138	0	8	12	16	--	11	0	0
	H	4&5	525	23	2	7	0	0	--	0	0	0

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			ACW RAIN									
VARIABLE & CATEGORY			Av	Sc	Pc	Pn	Tl	Ac	An	Sp	Lg	Ch
	L	<0,33	72	7	15	2	0	1	--	--	1	3
GSD	M	0,34-0,66	1394	210	248	77	10	16	--	--	0	12
	H	>0,66	825	121	90	36	16	3	--	--	0	8
	L	<33	194	27	51	5	0	0	--	--	1	3
VGH	M	34-66%	1658	261	269	87	8	9	--	--	0	11
	H	>66%	461	44	31	22	18	11	--	--	0	9
	L	<33%	813	95	43	18	8	4	--	--	0	1
%GC	M	34-66%	828	135	133	42	17	12	--	--	0	4
	H	>66%	650	102	175	54	1	4	--	--	1	18
	L	<0,33	121	24	14	15	0	0	--	--	0	6
TSD	M	0,34-0,66	1075	147	152	49	10	12	--	--	0	10
	H	>0,66	1095	167	187	51	16	8	--	--	1	7
	L	0-5	1338	172	174	45	15	10	--	--	0	9
TD0,5	M	6-10	403	86	69	16	3	1	--	--	1	3
	H	>10	550	80	110	54	8	9	--	--	0	11
	L	0-4	1561	222	251	87	21	19	--	--	0	16
TD1	M	5-10	586	84	61	28	5	1	--	--	1	5
	H	>10	144	32	41	0	0	0	--	--	0	2
	L	0-4	991	155	189	57	7	4	--	--	1	20
TD4	M	5-8	583	98	96	34	10	6	--	--	0	1
	H	>8	717	85	68	24	9	10	--	--	0	2
	L	0-2	1786	266	314	101	25	14	--	--	1	23
TD>4	M	3-5	403	51	38	12	1	3	--	--	0	0
	H	>5	102	21	1	2	0	3	--	--	0	0
	L	0&1	2291	338	353	115	26	20	--	--	1	23
ROC	M	2&3	0	0	0	0	0	0	--	--	0	0
	H	4&5	0	0	0	0	0	0	--	--	0	0
	L	0&1	1391	211	225	70	20	6	--	--	0	13
LIT	M	2&3	856	125	127	40	6	14	--	--	1	10
	H	4&5	44	2	1	5	0	0	--	--	0	0
	L	0&1	951	128	151	41	10	9	--	--	0	6
FOR	M	2&3	1129	172	184	47	8	11	--	--	1	16
	H	4&5	211	38	18	27	8	0	--	--	0	1

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Appendix IV: A comparison of various morphological measurements obtained from nine species of small mammal during the snap-trapping program and from general trapping around the Satara rest camp with the measurements obtained by Rautenbach (1982) for the same species trapped throughout the Transvaal. HT- total head to tail length (mm), T- tail length (mm), HF- hind foot length (mm), E- ear length (mm), M- mass (g), $\bar{x}$- mean, N- sample size, Min- minimum recorded, Max- maximum recorded.

	This Study				Rautenbach (1982)			
Saccostomus campestris								
Males	$\bar{x}$	N	Min	Max	$\bar{x}$	N	Min	Max
HT	151,8	6	142	165	165	93	130	236
T	36,6	6	33,2	40,0	41,7	93	29	87
HF	19,4	6	17,8	20,3	19,4	93	15	33
E	16,0	6	15,3	17,0	16,6	93	12	22
M	48,8	6	38,5	63,5	47,6	72	25	100
Females								
HT	166,6	8	134	174	166	105	133	195
T	39,5	9	35,8	45,7	41,1	105	26	58
HF	19,4	9	18,0	20,2	17,1	104	13	26
E	15,6	9	13,8	18,5	15,4	103	9	26
M	40,1	9	28,0	52,0	50,1	92	15	75
Tatera leucogaster								
Males	$\bar{x}$	N	Min	Max	$\bar{x}$	N	Min	Max
HT					276	482	210	321
T					148	493	121	173
HF					33,5	504	27	36
E					20,9	493	18	24
M					71,2	331	32	109
Females								
HT	238	2	226	250	278	541	225	330
T	127	2	119	135	149	531	120	175
HF	32,7	2	31,4	34,0	33,3	564	24	38
E	18,1	2	17,6	18,6	20,7	552	18	26
M	45,5	2	40	51	68,5	365	37	114
Lemniscomys griselda								
Males	$\bar{x}$	N	Min	Max	$\bar{x}$	N	Min	Max
HT	268	1			251	97	210	291
T	142	1			127	97	100	154
HF	30,7	1			27,1	97	22	31
E	16,6	1			16,1	97	12	19
M	61	1			56,2	75	32	89
Females								
HT					246	97	210	275
T					123	97	70	147
HF					27,0	97	23	31
E					16,1	97	12	19
M					51,8	80	27	74

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	This Study				Rautenbach (1982)			
Praomys natalensis								
Males	x̄	N	Min	Max	x̄	N	Min	Max
HT	189,6	15	133	247	202	721	150	254
T	92,6	15	61,5	122,3	96,2	700	75	131
HF	22,5	15	18,9	24,8	21,6	741	16	25
E	16,8	15	14,3	18,5	16,2	691	14	22
M	28,6	15	8,5	55,5	41,3	513	21	82
Females								
HT	185,2	21	118	227	198	648	150	245
T	89,2	20	56	114	93,5	646	73	125
HF	21,9	21	17,2	27,0	21,3	657	18	26
E	16,7	21	13,6	19,2	17,8	651	13	22
M	29,1	21	7,5	62,0	38,5	500	21	22
Praomys coucha								
Males	x̄	N	Min	Max	x̄	N	Min	Max
HT	187,2	5	157	205	Not recognised in Rautenbach (1982).			
T	84,5	5	64,5	98,2				
HF	21,9	5	21,4	23,1				
E	16,5	3	16,1	16,8				
M	29,4	5	19,5	39,0				
Females								
HT	154	8	129	204				
T	68,4	8	60	91,2				
HF	19,6	8	18,7	21,3				
E	15,4	7	14,0	16,3				
M	20,2	8	12,0	41,0				
Aethomys chrysophilus								
Males	x̄	N	Min	Max	x̄	N	Min	Max
HT	290	1			272	463	210	345
T	173	1			150	449	107	188
HF	29,2	1			27,7	459	22	32
E	20,8	1			19,9	450	16	23
M	77	1			76,7	331	38	112
Females								
HT					280	455	214	344
T					149	450	102	182
HF					27,4	477	20	33
E					20,8	471	16	24
M					68,1	344	26	125

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		This Study				Rautenbach (1982)			
Steatomys pratensis									
Males		x̄	N	Min	Max	x̄	N	Min	Max
	HT	129	1			130	39	117	157
	T	40,5	1			43,1	39	32	55
	HF	16,4	1			16,3	39	14	19
	E	13,8	1			14,1	38	10	16
	M	28,0	1			21,2	22	12	29
Females									
	HT	118	1			135	39	110	162
	T	38,6	1			43,8	39	33	53
	HF	17,2	1			16,2	39	14	19
	E	14,8	1			14,8	38	10	17
	M	16,0	1			25,3	22	10	44
Crocidura hirta									
Males		x̄	N	Min	Max	x̄	N	Min	Max
	HT					137,3	73	112	163
	T					48,3	73	39	62
	HF					14,7	73	11,5	16
	E					9,5	72	5	12
	M	17	1			16,1	26	11,1	24
Females									
	HT	115	2	96	134	136,7	71	110	155
	T	40,6	2	32,7	48,5	46,0	71	35	55
	HF	11,9	2	9,8	14,0	13,4	70	10	17
	E	7,5	1			9,4	70	5	12,5
	M	9,6	2	5,0	13,8	14,9	34	8	22
Elephantulus brachyrynchus									
Males		x̄	N	Min	Max	x̄	N	Min	Max
	HT	197,7	3	176	220	205,9	16	185	230
	T	90,1	3	65,4	110	96,3	16	85	112
	HF	29,5	3	28,3	30,4	28,1	16	26	30
	E	18,9	2	17,6	20,3	20,8	16	19	23
	M	37,8	3	33	42,5	43,6	8	39	55
Females									
	HT	170	1			212,4	28	177	230
	T	82,9	1			97,6	28	85	108
	HF	28,3	1			28,8	29	26	31
	E	20,0	1			20,0	28	17	22
	M	30	1			45,9	20	31	53

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Appendix V: Subjects for further study in small mammal ecology with a series of flow diagrams outlining the trapping requirements for spatial organization, community organization, activity, abundance, life-history parameters, population dynamics, microhabitat preferences and diet composition. M-R = mark-recapture, I.S. = instaneous sample (single sample), Stratified random configuration see Price & Kramer (1984). Additional references used in the subsequent diagrams but not referred to in main text are given below.

GAUCH, H.G. 1982. Multi-variate analysis in community ecology. Cambridge Univ. Press, Cambridge.

HANSSON, L. 1970. Methods of morphological diet micro-analysis in rodents. Oikos 21:255-266.

MOHR, C.O. & STUMPF, W.A. 1966. Comparison of methods for calculating areas of animal activity. J. Wildl. Mgmt. 30:293-304.

PRICE, M.V. & KRAMER, K.A. 1984. On measuring microhabitat affinities with special reference to small mammals. Oikos 42:349-354.

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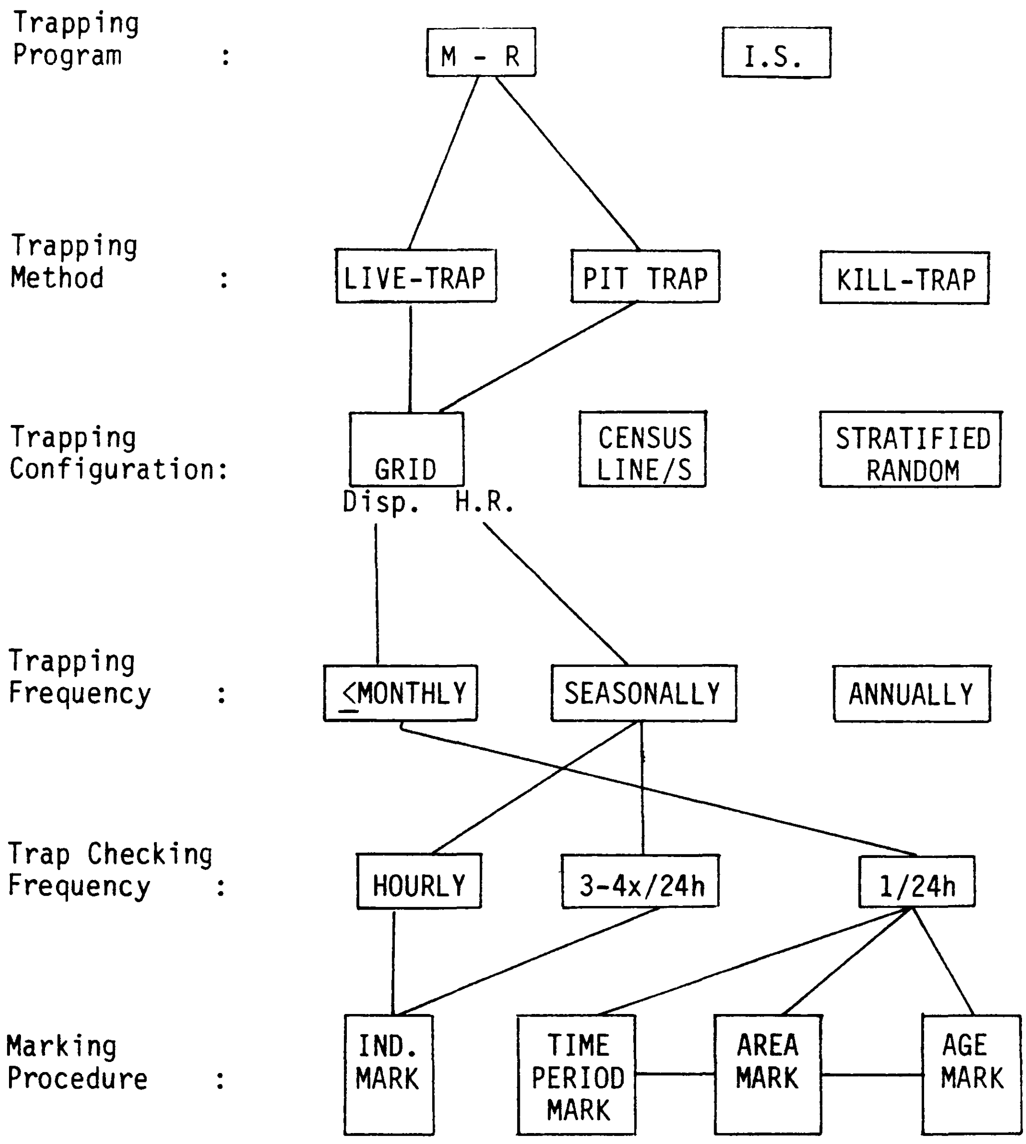
Proposed Objective: SPATIAL ORGANIZATION
Home range & Dispersal



Analytical Methods : see De Blase & Martin (1981)
Stickel (1954)
Mohr & Stompf (1966)

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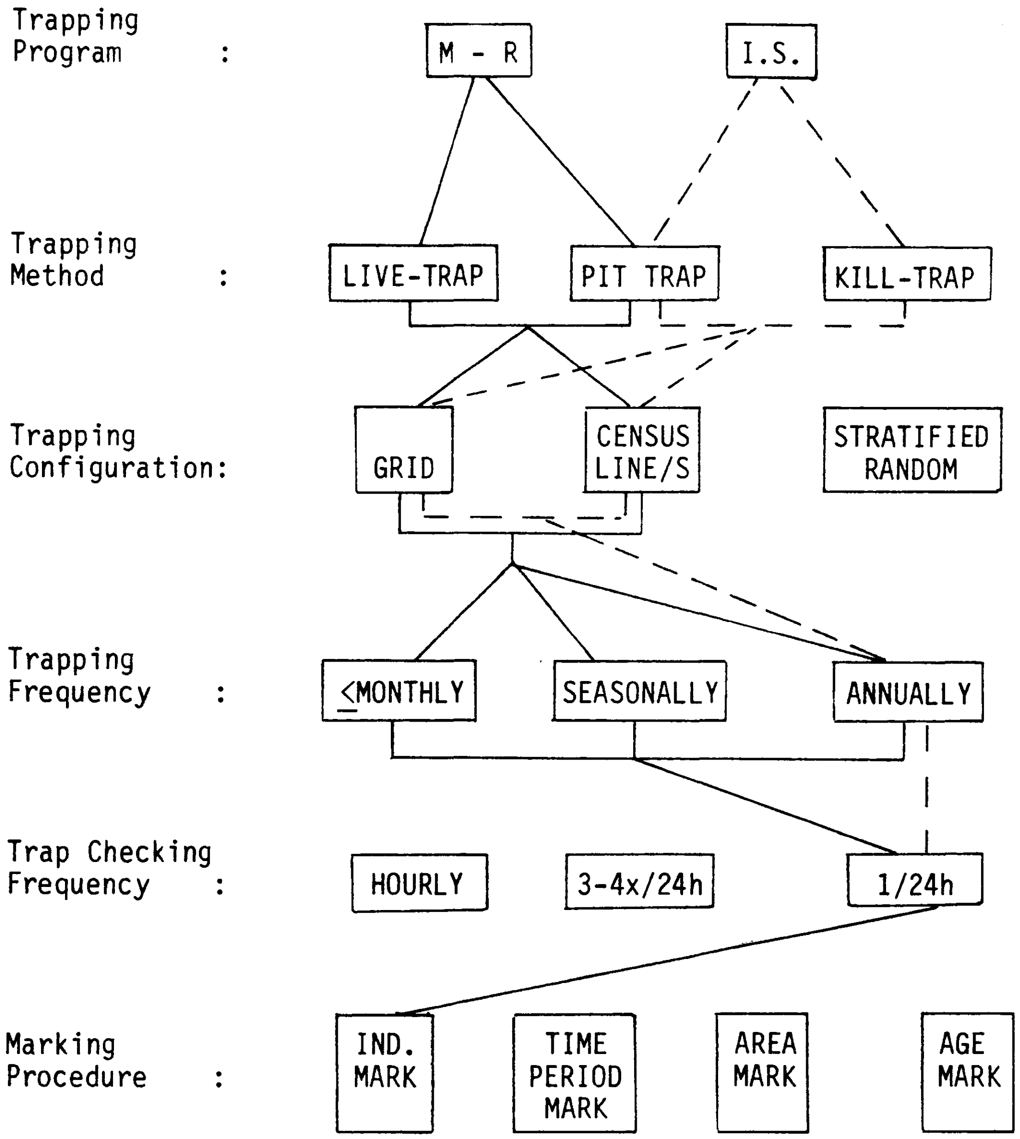
Proposed Objective: ABUNDANCE



Analytical Methods	: Numbers	Density n/ha
	M-R Jolly-Seber Schumacher	Assessment lines (O'Farrell *et al.* 1977) Boundary strip (Stickel 1954)
	I.S. Zippin	Mean Maximum Distance Moved (Anderson & Wilson 1985)

(see Caughley 1977)

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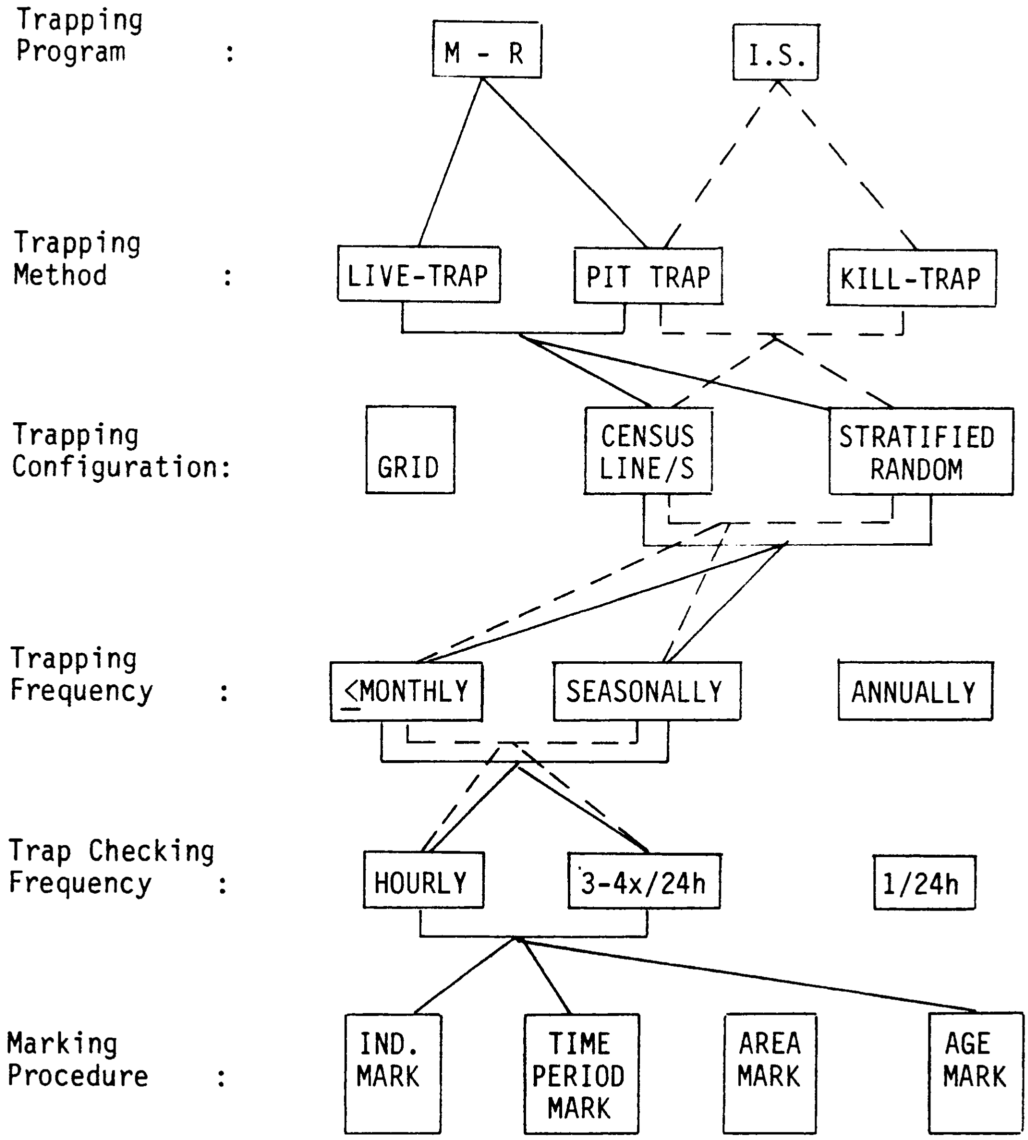
Proposed Objective: ACTIVITY



Analytical Methods :

SUGGESTIONS : Activity in relation to - 24 hour period
Lunar cycle
Weather conditions
Predator activity

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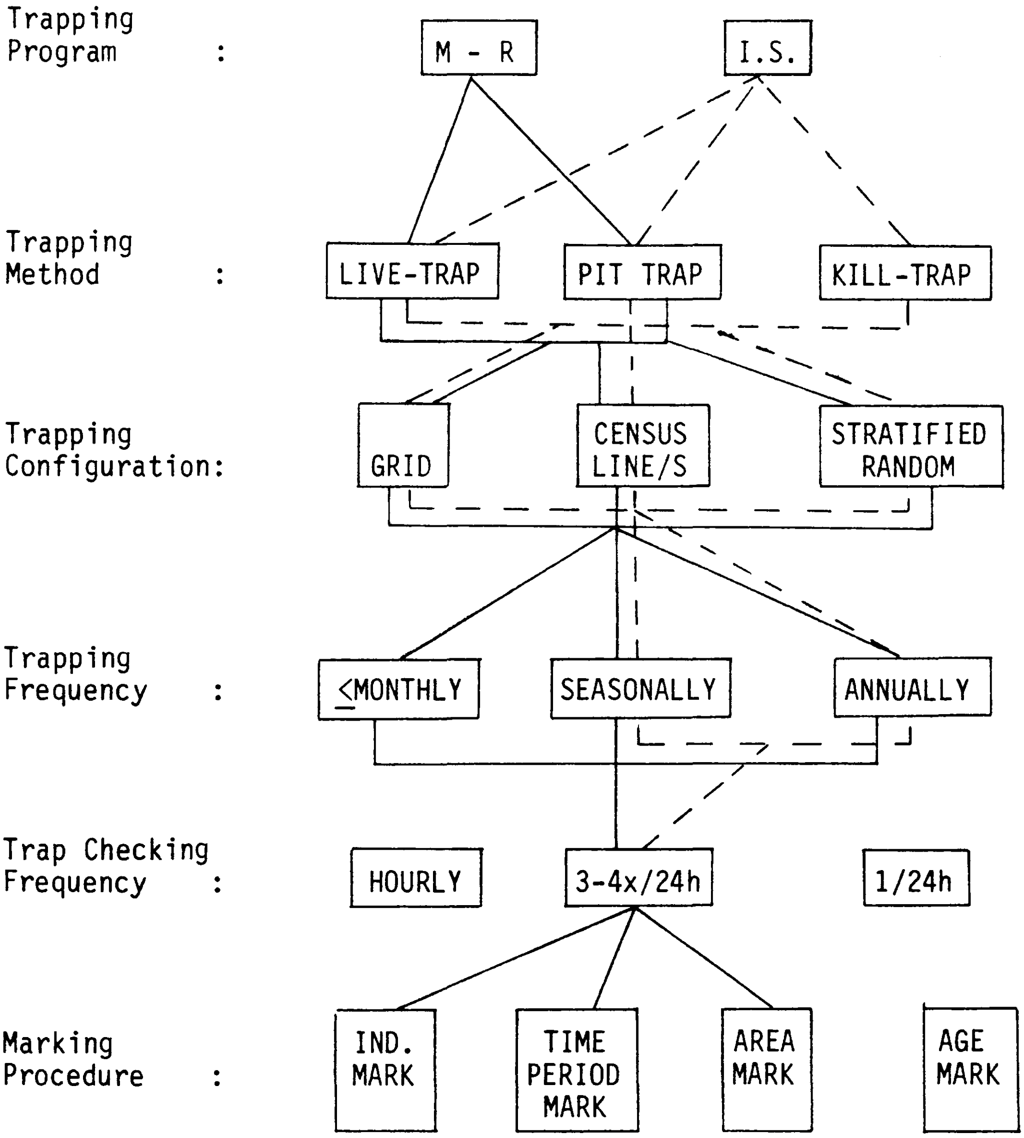
Proposed Objective: COMMUNITY ORGANIZATION



Analytical Methods :

SUGGESTIONS : Community composition
Species diversity
Biomass diversity

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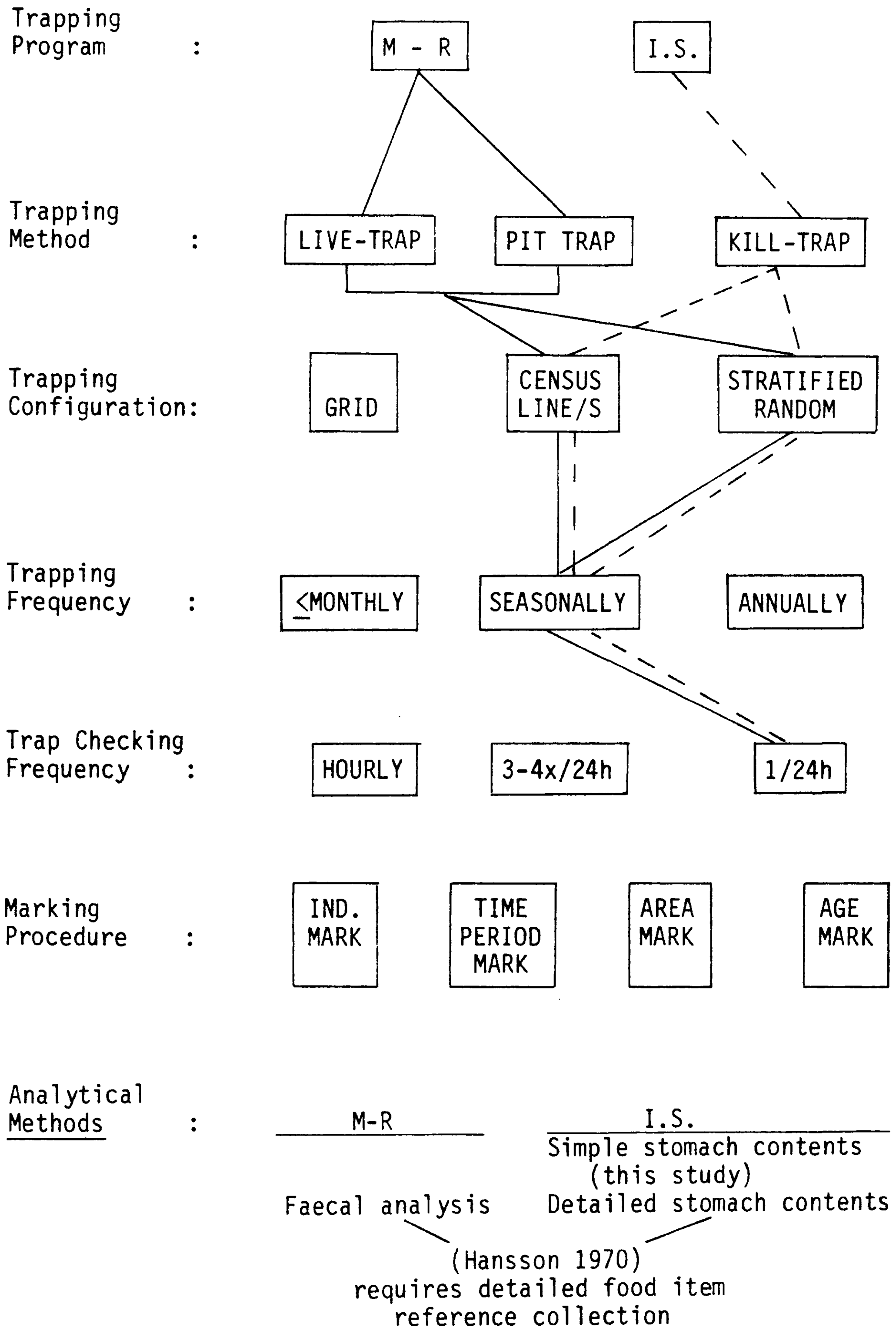
Proposed Objective: DIET COMPOSITION



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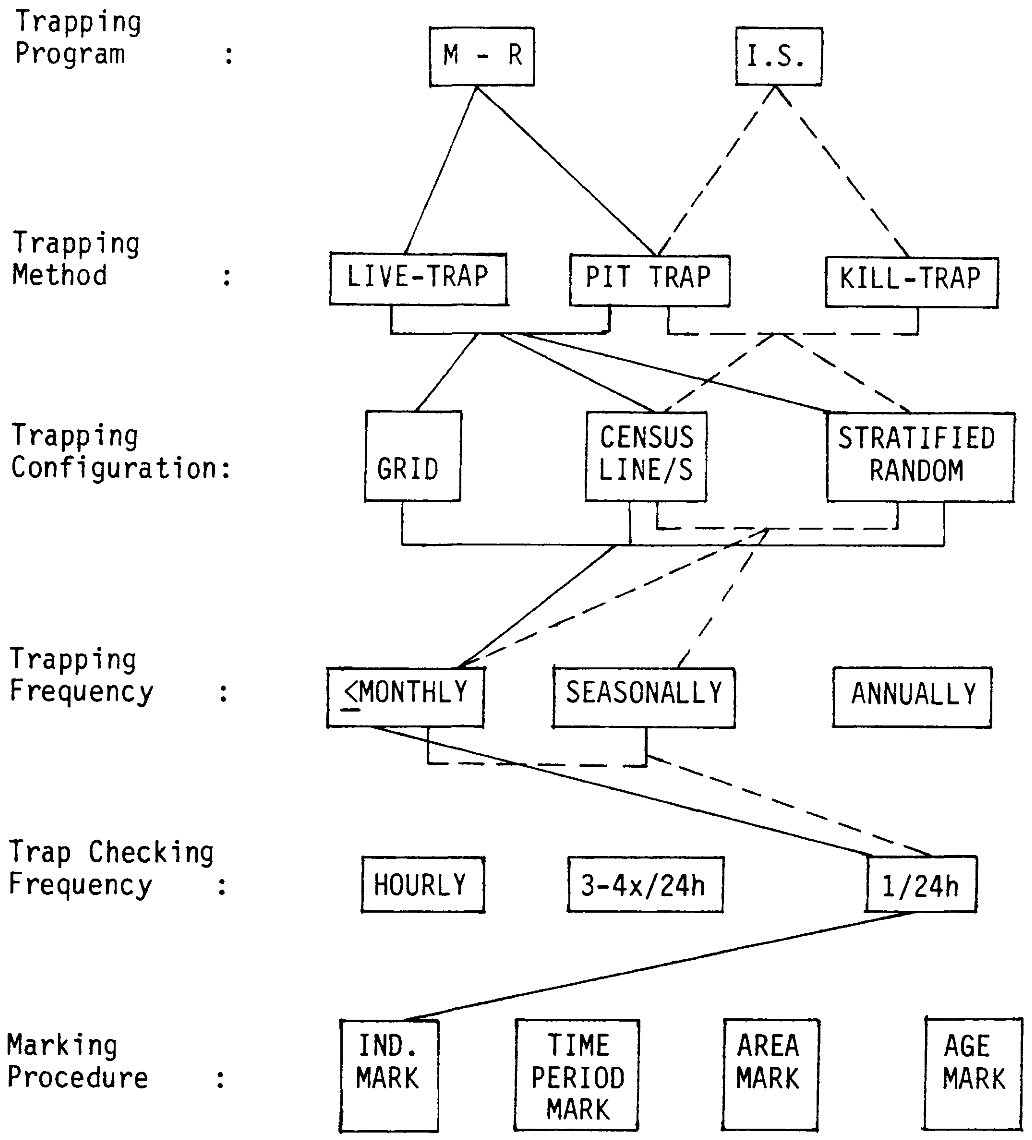
Proposed Objective: LIFE HISTORY PARAMETERS



Analytical Methods :

M-R	I.S.
Birth, mortality, survival, fecundity (Jolly-Seber)	Reproductive activity/ potential, no. embryos present/resorbed Age structure toothwear (De Graaff 1981) eye-lense weight (De Blase & Martin 1981) morphological measurements

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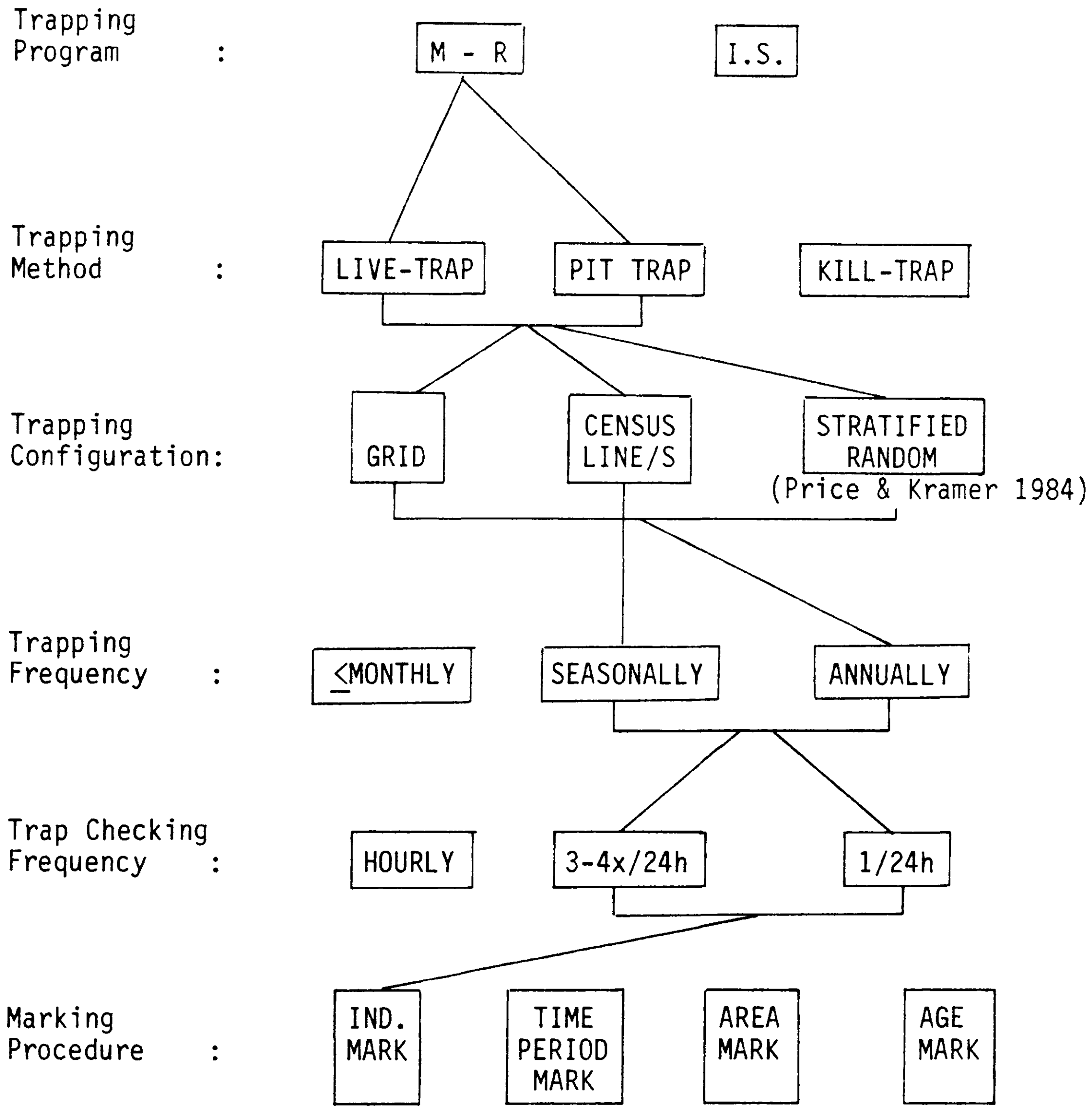
Proposed Objective: MICROHABITAT PREFERENCES



Analytical <u>Methods</u> : Statistical analyses
Multi-variate analysis (Gauch 1982)
principal components analysis
correspondence analysis
Chi-square analysis (Zar 1984)
Kolmogorov-smirnove (Zar 1984)

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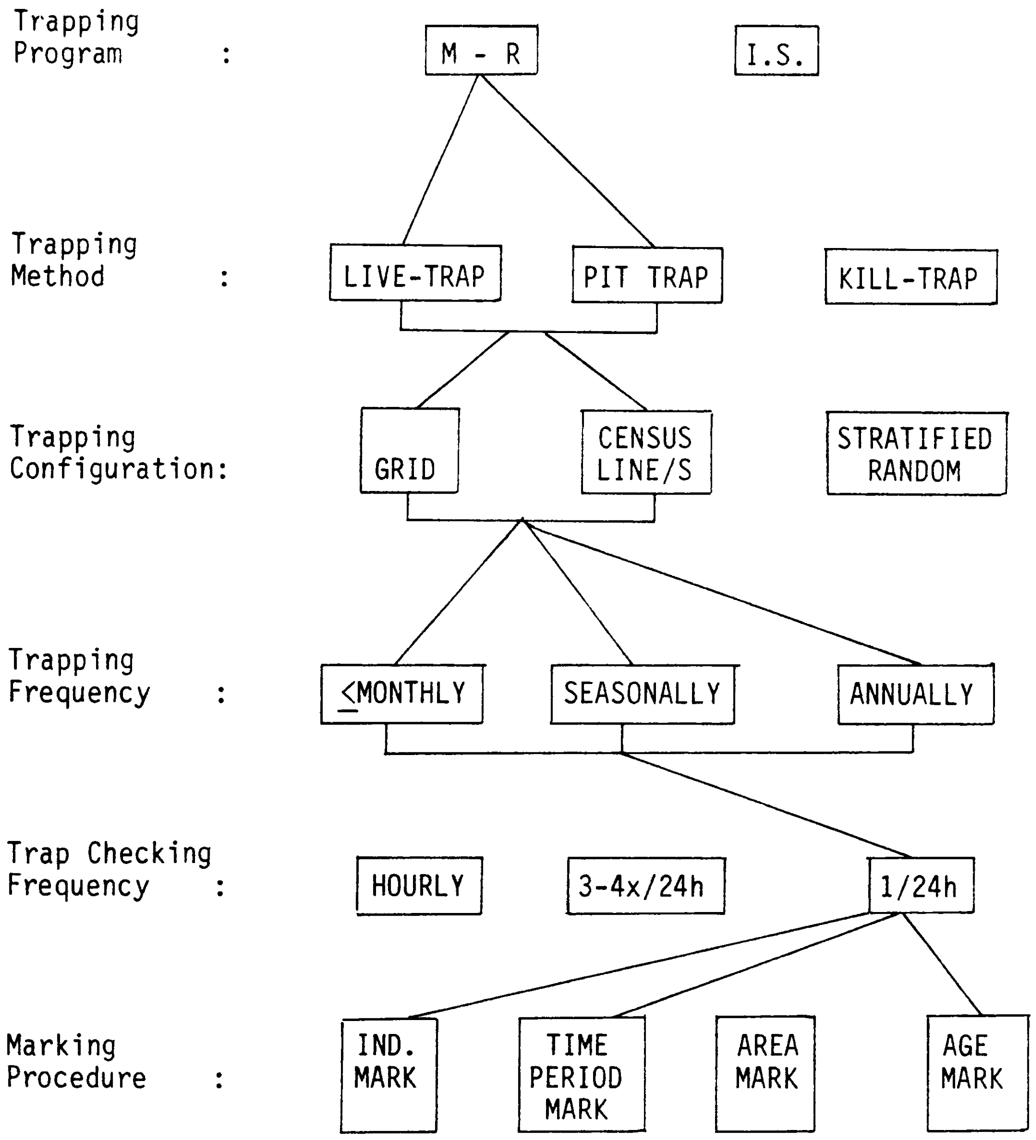
Proposed Objective: POPULATION DYNAMICS



Analytical Methods : Density assessment (see Abundance methods)

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Small-mammal trapping: analysis of disturbance and methods of trap protection

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Trapping results from a two-year study of small-mammal populations in the Kruger National Park were analysed in terms of disturbance and damage to traps and captive mortality. Black-backed jackals, *Canis mesomelas*, and tree squirrels, *Paraxerus cepapi*, were the major causes of disturbance in the two different areas. Methods of trap protection are discussed and the design for a jackal-proof unit given. Field experiments showed no significant difference between small-mammal captures with and without the units. The trap protectors were 100% effective against jackal disturbance and appeared to reduce disturbance by other factors.

S. Afr. J. Wildl. Res. 1985, 15: 54 – 58

Gedurende 'n twee-jaar studie van kleinsoogdierbevolkings in twee habitatte van die Nasionale Krugerwildtuin, was vangsteuring die hoof probleem. Vangresultate is ontleed in terme van steuring, skade en mortaliteit. Die rooijakkals, *Canis mesomelas*, en boomeekhoring, *Paraxerus cepapi*, was hoofsaaklik verantwoordelik vir die steurings in die onderskeie gebiede. Metodes van beskerming van die valle word bespreek en die ontwerp van 'n jakkalsbestande eenheid word beskryf. Veldeksperimente het geen betekenisvolle verskille tussen kleinsoogdiervangste binne of buite die eenhede getoon nie. Die valbeskermers was 100% effektief teen jakkalse en het geblyk om steuring deur ander faktore te verminder.

S.-Afr. Tydskr. Natuurnav. 1985, 15: 54 – 58

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Received 1 February 1985; accepted 21 February 1985

Introduction

Trap disturbance is often a common but unpublished problem in many small-mammals studies. The degree of disturbance can range from an occasional irregular happening to premeditated nightly forays of destruction. The consequences of serious trap disturbance can bring a study to a complete halt for several reasons: trap unavailability owing to closure, damage or loss, cost in time and money for repair or replacement of traps and captive mortality. These have direct effects on the validity of the results obtained for population size, mortality rates, density estimates, spatial movement and home-range estimates.

Depending on the aims of the study and the source of the problem, there are three options for a solution: (i) to change the trapping site, hoping to leave the problem behind; (ii) to remove the problem animal from the study site; (iii) to enclose the traps in such a way as to protect them but still allow free access for the small mammals.

This paper describes trap disturbances which jeopardized a study on the ecology of small mammals in two habitats in the Kruger National Park. The causes of disturbance, their influence on the study and the methods of trap protection are discussed. The construction, use and effectiveness of a trap protector are described.

Materials and Methods

This study was conducted in the Satara region of the Kruger National Park. Small-mammal community ecology was compared in two habitat types, namely the Marula/Knobthorn *Sclerocarya caffra*/*Acacia nigrescens* savannah (MKn) and the *Acacia welwitschii* thickets (Acw) as described by Gertenbach (1983). These habitats are characterized by a uniform grassland with few large trees in MKn and a mosaic of woodland, vlei and grassland in Acw.

During 1982 – 1984, trapping was conducted three times per year in each habitat, in November/December, March/April and July/August. The three trapping periods roughly coincided with a spring, late summer, and winter season which resulted in six trapping sessions during the study. Two sites in each habitat were trapped alternately (i.e. MKnI, AcwI, MKnII, AcwII) for 6 to 10 nights each. In most cases, trapping was avoided for a five-day period around full moon. Sherman live traps (230 × 77 × 92 mm) were used at all times. Approximately 90 traps per night with 20-m spacing were set in two parallel lines 50 m apart. Data from the two trapping sites in each habitat were combined to provide the results presented here. If an animal was responsible for trap disturbance, it was identified to species whenever possible by

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recording what was captured in the trap, examining trap damage or by identifying the spoor around the trap. In some cases, the cause was an environmental factor such as weather and if the cause was unknown, it was recorded as such. Captive mortalities were assumed when urine/faeces or hair were found in predator-damaged traps.

The rainfall was recorded in each habitat using a rain gauge. The grass biomass was estimated using the disc pasture meter method evaluated by Danckwerts & Trollope (1980).

The field experiment for small-mammal captures in traps with and without the trap protectors were conducted in two areas approximately 10 km from the main trapping sites. Concurrently in each area, 40 traps at 30-m spacings were set in two parallel lines 20 m apart. Every other trap was enclosed in a trap protector and the counterpart of each trap across the parallel lines had the opposite treatment. As the results from the two areas were similar, the data was combined.

All data being compared were subjected to a modified χ^2 test for two categories with the Yates correction for continuity (Brower & Zar 1977).

Results and Discussion

A summary of captures during the six trapping sessions conducted in MKn and Acw is provided in Table 1. The number of trapping nights in Session 6 was reduced because of the need to conduct assessment line trapping while still avoiding the full-moon period. Other variations in the number of trap nights were due to trap disturbance and the need to limit ‘trap-happy’ animals monopolizing one specific trap (i.e. if the same individual was caught two nights running in the same trap, the trap was then removed for one night).

The number of traps disturbed in both habitats was not significantly different ($\chi^2 = 0{,}270$; $P > 0{,}50$). Trap damage and mortality were significantly higher in MKn ($\chi^2 = 59{,}04$ and 30,02 respectively; $P < 0{,}001$). Most of the disturbance and damage in both habitats occurred in the first four sessions. At the start of this study, the Kruger Park, along with most of southern Africa was experiencing a year of drought. The mean grass biomass measured showed poor grass growth until sometime between the fourth and fifth sessions, when the drought broke.

In the first four sessions, MKn showed a tendency for traps disturbed and damaged to decrease with each session, while captive mortality increased. By Session 4, 53% of the individuals captured in that session had been recorded as mortalities. In contrast, during the first four trapping sessions of Acw, disturbance and damage increased to a peak in Session 3 while mortality remained negligible. Grass biomass was at its lowest level in both areas in Session 3.

The causes of disturbance are shown in Table 2. Black-backed jackals and bush squirrels were the two major problem animals in the MKn and Acw respectively. Other species individually had such a minor influence on trap disturbance that they were grouped into the remaining categories. The environmental factor which caused the most disturbance and damage was heavy rain while mortality in traps resulted from both heat stress and, especially in the case of shrews, chill. Also included in the environmental category were four trap-induced deaths. These occurred when animals were only partially captured and usually when more than one individual attempted to enter a trap at the same time. Unknown disturbance especially in the Acw was often thought to be due to ants moving the bait onto the treadle but as this was not absolutely certain, these incidences, (probably over 50%), were recorded as unknown.

Ignoring the unknown category, the main cause of disturbance in each habitat was different. Whereas jackals caused 79% of all known distrubances in MKn, they caused only 7% in Acw. Squirrels caused < 1% in MKn but 38% in Acw. The difference in squirrel disturbances was most likely due directly to their relative abundance. MKn, with its few large trees, had an extremely low number of squirrels present while the Acw woodland area harboured many. The large difference in the jackal disturbance was the result of a learned behaviour in a group local to the MKn trap lines and not related to their relative abundance. For the other four categories, the total disturbance caused was similar in both habitats. Large mammals disturbed traps in both habitats, these disturbances being due to greater elephant utilization of the area local to the trap sites. Large mammals disturbed

Table 1 Summary of small-mammal trapping results over six sessions

	Sessions in MKn							Sessions in Acw						
	1	2	3	4	5	6	Total	1	2	3	4	5	6	Total
No. trap nights	1,728 (18)[a]	1,764 (20)	1,602 (19)	1,433 (17)	1,415 (18)	923 (12)	8,865 (104)	1,728 (18)	1,780 (20)	1,763 (20)	1,544 (18)	1,434 (18)	949 (12)	9,198 (106)
No. small mammals caught[b]	35	54	70	66	288	395	908	28	36	36	51	199	208	558
No. traps disturbed	90	375	185	137[d]	12	11	805	181	139	235	163	77	29	827
No. traps damaged	1	108	41	22	2	0	185	2	11	22	1	4	0	63
No. known mortalities	1	0	6	35	6	1	49	0	1	0	0	2	4	7
Rainfall (mm)[c]	40	10	24	100	0	0		?	>100	0	104	144	47	
$\bar{x}$ grass biomass (g/m^2)	175	188	155	157	344	389		202	169	129	148	327	299	

[a]( ) No. of nights trapped. [b] Total no. of individuals only, not including recaptures. [c] Records for rain which fell only while trapping that area. [d] Initiation of trap protectors in MKn only. Sessions 1 and 4 — spring sessions. Sessions 2 and 5 — summer sessions. Sessions 3 and 6 — winter sessions.

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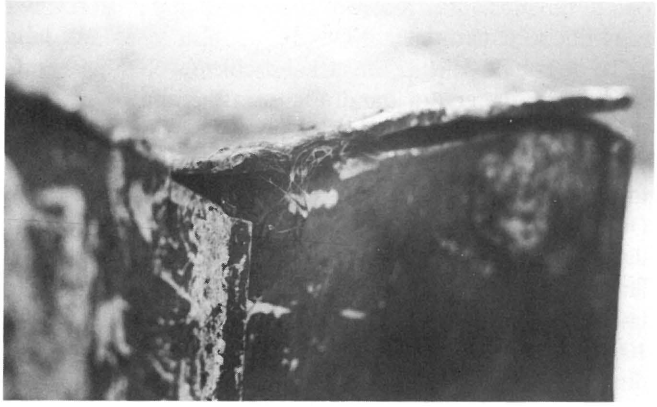

Figure 1 A learned 'door-opening technique' was inferred from the minor damage and small-mammal hair on the top edge of traps in the MKn area after Session 3.

(four months later) the same technique was used and by the end of that session, they were disturbing only those traps which had a captive. Table 1 shows that the level of trap damage progressively decreased while mortality increased as their technique of trap opening improved. Various easy solutions were tried at first. These included closely tying the traps down to a stationary object; covering with *Acacia* sp. branches; sprinkling the traps with cayenne pepper or periperi sauce and booby-trapping a high percentage of the traps with a stretched rubber strap (inner tube) which upon trap movement was released at one end. The latter caused a reduction in disturbance for one night but thereafter, disturbance again increased and not only were the captives eaten but so were the rubber straps.

Night-time observations by a member of the Parks Board staff confirmed our early morning sightings of three jackals in the immediate vicinity of the trap lines. The Parks Board undertook to remove the individual who they thought was the culprit. On the morning following the night of the successful removal (21h00), all trap captives but one had been eaten. The technique of door opening had either been learned by the other jackals or the wrong individual had been removed. Removal of the natural predators is not the ideal solution to the problem however as their removal upsets the natural ecological balance as much as the abnormal mortality of the small mammals (Getz & Batzli 1974).

A solution was found in the design and construction of a trap protection unit. This trap protector and mirror stick were designed and successfully used without prior knowledge of the Getz & Batzli (1974) device.

Figure 2 shows the design of the trap protector and a mirror stick which greatly aided trap checking each morning. The protector was made from galvanized steel downpipe, made and cut to size by a local plumbing shop. Using a hinge and poprivets, a door of galvanized soft steel sheet was attached to one end while a single large hole was drilled through the top and bottom surfaces at the opposite end. The door allowed easy researcher access to the trap inside while a stake was fitted through the holes in the other end and hammered into the ground. This secured the protector and stopped the jackal from pulling the trap out while still allowing the small mammal free access to the trap inside. The length of the downpipe was sufficient to prevent the jackal from reaching the trap. As Getz & Batzli (1974) point out, morning trap inspection did prove to be quite tedious, so the mirror stick was designed to reveal trap condition (open or closed) and the presence or absence of bait. This greatly facilitated the checking of traps. Its use was limited though when grass thickness became so great that there was little available light at trap level to give a good reflection. This caused little problem in the present study as by that time trapping success rate was between 95 and 105%. The mirror stick was made out of two pieces of 1,5-cm aluminium pole. A mirror, large enough to allow a full reflection of the trap was attached to the short pole and these two pieces were loosely bolted together. A spring was attached at the back of the mirror section to allow easy adjustment for the correct reflecting position while resting the mirror on the ground.

Before the trap protectors were used in the main study,

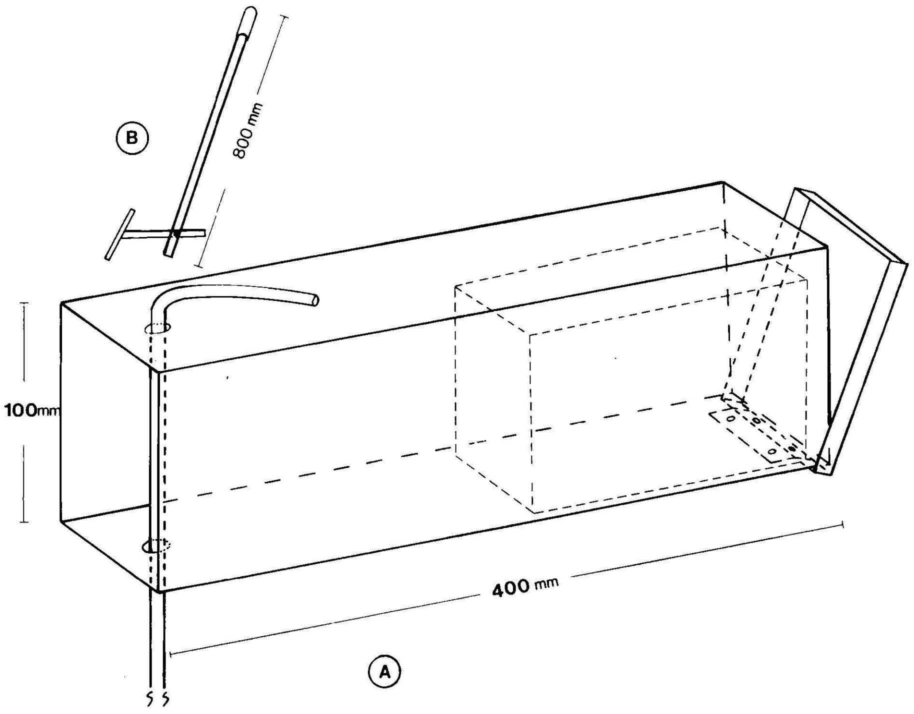

Figure 2 (a) Trap protector construction; (b) mirror stick.

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Identification of cryptic species of rodents (*Mastomys*, *Aethomys*, *Saccostomus*) in the Kruger National Park

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Mastomys natalensis, Aethomys chrysophilus and *Saccostomus campestris* are three common and widespread rodent species in the Kruger National Park. Chromosomal and protein electrophoretic investigations reveal that these species are in fact complexes of morphologically similar, though genetically distinct, species. Their respective distributions in the Kruger National Park are reported and species diagnostic characters (diploid chromosome number, genitalia, spermatozoa and electromorphs) are presented for the practical identification of the cryptic species. The value of a genetical approach to resolving cryptic species is emphasized with respect to ecological studies.

S. Afr. J. Zool. 1986, 21: 95–99

Mastomys natalensis, Aethomys chrysophilus en *Saccostomus campestris* kom algemeen en wydverspreid in die Nasionale Krugerwildtuin voor. Chromosoom- en elektroforetiese studies dui aan dat hierdie spesies in werklikheid komplekse van morfologies eenderse maar geneties onderskeibare spesies is. Hul verspreidingsgebiede binne die Krugerwildtuin en hul diagnostiese kenmerke (diploïede chromosoomgetal, genitalia, spermatosoa en elektromorfe) word gegee om die identifikasie van die onderskeie sibbespesies te vergemaklik. Die nut van 'n genetiese benadering word beklemtoon, veral ten opsigte van ekologiese studies.

S.-Afr. Tydskr. Dierk. 1986, 21: 95–99

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Faunal surveys of National Parks are considered of prime importance as the basis for effective conservation and management of animal populations (Pienaar 1984). In the case of large mammals, species identification does not present a particular problem. By contrast, small mammals and especially rodents pose numerous unresolved questions concerning their distribution, ecology and species identification despite the fact that they have been the subject of a number of major taxonomic and zoogeographic studies in southern Africa (Pienaar, Rautenbach & De Graaff 1980; De Graaff 1981; Rautenbach 1982; Lynch 1983; Smithers 1983).

Accurate identification of rodent species is problematical because a phenetic approach which traditionally involves the comparison of morphological features such as pelage colour or cranial features may not resolve the differences between cryptic, but genetically distinct, species. The problem may be resolved if a genetic concept of species is considered.

In this sense, species are defined in terms of positive assortative mating between conspecifics or in population genetic terms, as a gene pool or 'field for gene recombination' (Carson 1957). Recent studies on southern African rodents have revealed that the taxa *Aethomys chrysophilus*, *Mastomys natalensis* and *Saccostomus campestris*, are species complexes (Gordon & Rautenbach 1980; Green, Keogh, Gordon, Pinto & Hartwig 1980; Gordon in press). In the case of *Mastomys*, the nomenclatural problems have been resolved with reference to the genetic species: *M. coucha* is characterized by a diploid chromosome number (2n)=36 and 'fast' double-banded haemoglobin electromorph and *M. natalensis* by 2n=32 and 'slow' haemoglobin electromorph relative to a human standard. The distribution of these cryptic species is known generally for southern Africa but not specifically for Kruger National Park. *Aethomys chrysophilus* was recognized as a species complex based on chromosomal data from sympatric populations; no intermediate chromosomal forms were detected in nature. Gordon & Rautenbach (1980) proposed that *A. chrysophilus* specimens with 2n=50 be referred to *A. chrysophilus sensu stricto* and those with 2n=44 as *A. chrysophilus* sp. B. Systematic and nomenclatural aspects of the *Aethomys* group are currently under study by D. Visser (in prep., M.Sc. thesis). On the basis of chromosomal, biochemical and zoogeographic data, the taxon *S. campestris*, formerly recognized as a monotypic genus in southern Africa, is now considered to comprise at least two genetic species which are tentatively referred to as sp. A and sp. B (Gordon in press).

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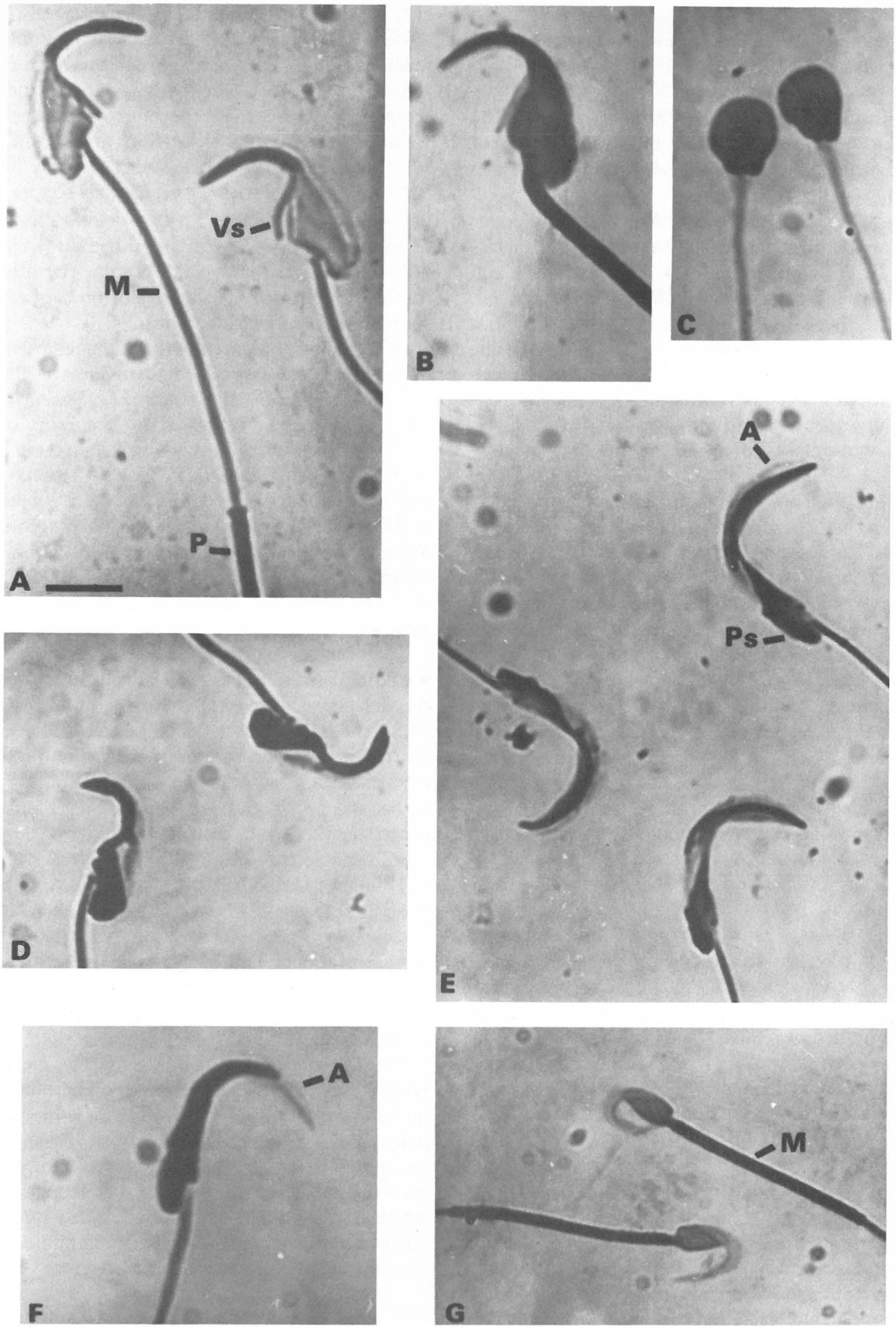

Figure 3 Spermatozoa of *Aethomys*, *Mastomys* and *Saccostomus* specimens from the Kruger National Park. (A) Silver-nitrate stained spermatozoa of *A. chrysophilus* (2n=50) showing differentially stained head with ventral spike (Vs), tail midpiece (M) and part of principal piece (P). (B) Giemsa-stained head of *A. chrysophilus* (2n=50). (C) Giemsa-stained spermatozoa head of *A. chrysophilus* sp. B (2n=44) which shows the extreme shape difference between the *chrysophilus* cryptic species. (D) Silver-nitrate stained spermatozoa head of *A. namaquensis*. (E) Silver-nitrate stained head of *M. natalensis* showing acrosome (A) and postacrosomal sheath (Ps). (F) Giemsa-stained head of *M. natalensis*. (G) Giemsa-stained head of *S. campestris*. Scale bar in A is approximately 10 μm for A–F.

Aethomys spp.

Initial cytogenetic analysis of *A. chrysophilus* s.l. in the *Acacia welwitschii* area showed that specimens were *A. chrysophilus* sp. B (2n=44), the widely distributed South African species (Gordon & Rautenbach 1980). *A. chrysophilus* s.s. (2n=50) and *A. namaquensis* were subsequently found in sympatry in the Klopperfontein area north of Punda Maria Camp. Although specimens with 2n=50 had

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Close chromosomal congruence in two species of ground squirrel: *Xerus inauris* and *X. princeps* (Rodentia: Sciuridae)

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Chromosomes from cultured fibroblasts of two southern African ground squirrel species, *Xerus inauris* (2n = 38) and *X. princeps* (2n = 38), were compared using G-banding, C-banding and silver nitrate staining for the detection of NORs (nucleolar organizer regions). The karyoptypes of the two species, whose taxonomic status is the subject of some uncertainty, are largely identical except for a subtle heterochromatic difference which affects a single autosomal chromosome pair in *X. inauris*. The species specificity of this marker in their zone of contact indicates an absence of gene flow between these taxa and gives credence to the recognition of *X. inauris* and *X. princeps* as two biologically distinct species.

S. Afr. J. Zool. 1986, 21: 100–105

G- en C-band gekleurde chromosome afkomstig van fibroblaskulture van twee Suid-Afrikaanse grondeekhoringspesies *Xerus inauris* (2n = 38) en *X. princeps* (2n = 38) is vergelyk. Daar is ook gebruik gemaak van 'n silvernitraatkleuringstegniek vir die identifikasie van die nukleolus organiserende gebiede van die chromosome. Die kariotipes van die twee spesies, waarvan die taksonomiese status onseker is, is byna identies behalwe vir geringe verskille in heterochromatien ten opsigte van een outosomale chromosoompaar in *X. inauris*. Die spesiespesifisiteit van hierdie chromosoommerker dui op die afwesigheid van geenuitruiling tussen die taksa in hulle geografiese kontakgebied. Hierdie data ondersteun dus die huidige klassifikasie wat *X. inauris* en *X. princeps* as twee afsonderlike spesies beskou.

S.-Afr. Tydskr. Dierk. 1986, 21: 100–105

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Received 5 August 1985; accepted 16 September 1985

The family Sciuridae to which the terrestrial, arborial and flying squirrels belong comprises two subfamilies, the Sciurinae and the Petauristinae. In view of an almost cosmopolitan distribution and the wide variety of habitat types associated with the family, squirrels are particularly suited to studies of speciation processes and adaptations involving contrasting environments.

Two terrestrial squirrel species (subfamily Sciurinae) occur in the southern African subregion. The more widespread of the two, the Cape ground squirrel, *Xerus inauris*, has the greater part of its distributional range confined to the south-western arid zone (Figure 1A), while the mountain ground squirrel, *X. princeps*, is associated primarily with the Namibian western escarpment and the south-western parts of Angola (Figure 1B; Smithers 1983). Although both taxa are found exclusively in arid areas, they rarely occur sympatrically, *X. inauris* being replaced in extreme north-west Namibia by *X. princeps*. Moreover, casual observations tend to support Shortridge's (1934) claim that the former taxon shows a preference for open terrain associated with sparse bush, while *X. princeps* is a rock-dwelling species.

Although generally regarded as being morphologically distinct (Amtmann 1975; Smithers 1983), the recognition of the taxa as separate species is accepted with reservation by De Graaff (1981). In an attempt to provide definitive data on the taxonomic status of these species and to illustrate factors possibly contributing to the maintenance of species integrity in their contact zones, a multidisciplinary investigation employing karyotypic, craniometric, behavioural and ecophysiological parameters was initiated. The cytosystematic data form the basis of this report.

Material and Methods

The species, number of specimens studied and grid reference to the collection localities are as follows:

X. inauris: 3 ♂♂, 2 ♀♀; Farm Klein Spitzkopp 45 km west of Usakos (22°00′S/15°33′E), Namibia.

X. princeps: 2 ♂♂, 2 ♀♀; Farm David Ost 18 km north of Usakos, Namibia.

All animals examined in the present study were deposited as voucher specimens in the mammal collection of the Transvaal Museum, Pretoria.

Metaphase cells were obtained from fibroblast cultures initiated from skin biopsies and disaggregated kidney tissue using standard procedures. Air-dried slides were prepared from cultured cells and subsequently G- and C-banded using

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Observations on the post-natal development of the tiny musk shrew, *Crocidura bicolor*

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Received 23 April 1986; accepted 10 June 1986

Crocidura bicolor is the smallest of southern Africa's *Crocidura* shrews and little is known of its biology. A female, captured in the Kruger National Park, was observed giving birth to two young. The post-natal development of the young reported here was slower than the two previously published incidences. Suggested reasons for the discrepancies are the differential diets of the mothers, their geographical origins and the smaller size of this female.

Crocidura bicolor is die kleinste *Crocidura*-skeerbek in suidelike Afrika en min biologiese inligting is oor hulle beskikbaar. 'n Wyfie wat in die Nasionale Krugerwildtuin gevang is, is waargeneem terwyl sy geboorte geskenk het aan twee kleintjies. Die na-geboortelike ontwikkeling van die kleintjies waarvan hier verslag gedoen word, was stadiger as twee vorige gepubliseerde gevalle. Voorgestelde redes vir die teenstrydighede is die onderskeie diëte van die moeders, hulle geografiese herkomste en die kleiner grootte van hierdie wyfie.

Crocidura bicolor, the tiny musk shrew, is rarely captured because of its extremely small size (3 – 4 g). Most available information is in the form of scattered locality records and morphological measurements (Meester 1963; Rautenbach 1982; Smithers 1983). Ansell (1964) and Dippenaar (1979) have reported on single incidences of post-natal development of this species but no detailed study appears to have been published. Further published information on this rare species is very necessary.

In March 1983, during severe drought conditions, two *Crocidura bicolor* (3,1 g; 2,5 g) were live-trapped (Sherman aluminium live-trap, 230 × 90 × 72 mm) in sparsely covered grasslands, approximately 20 km east of Satara, Kruger National Park. Their presence in that eastern region had previously been established by Coetzee (1963) from owl pellet analysis. The larger individual was retained for identification purposes. Upon her death, seven weeks later, she was identified, using cranial characteristics, as a *Crocidura bicolor* (TM 35905) by the Transvaal Museum. She was extremely small even for this species (Dippenaar *in litt.*) though Meester (1963) notes that specimens from the Transvaal lowveld appear to be smaller than those from elsewhere.

While in captivity, the female gave birth and she and the young were kept in a small plastic laboratory mouse cage, the floor of which was covered with a layer of soil. Rocks, cut grass and a small cardboard tube placed in the cage were regularly used by the female in daily activity. However, none were chosen for nest placement. Instead, she made a slight hollow in the corner of the cage. Water was provided *ad libitum* and a varied live insect diet was provided 2 – 3 times per day. The diet offered was dependent upon our previous night's insect catch. Preferred items were moths, grasshoppers, locusts, caterpillars, cockroaches, praying mantes, dragonflies and crickets. Mealworms, used as a supplement when insect catches were low, were not preferred and dung beetles were refused.

On March 14, at 22h50 the female gave birth to two offspring (sexes undetermined). Parturition of the first young was not seen but that of the second was followed to completion. A typical parturition posture was observed where the female frequently turned and licked her vulval region. When the neonate was partially emerged, she gripped it with her teeth and pulled it out. Twenty minutes elapsed after parturition before she collected the two pups and settled down to suckle.

Physical development of the young was recorded by mass (g) and body length measurements (mm). Initially, the young were weighed using a 100 g Pesola spring balance until a more sensitive triple-beam balance was obtained. The mass of the mother was measured at the same time as that of the young. All length measurements reported are the average of three or four measures taken with Vernier callipers. The physical and behavioural development of the young from Day 0 (birth) to Day 29 are presented in Table 1. At birth, the offspring were totally naked with eyes and ears closed. Movement was uncoordinated but soft squeaks were emitted whenever the mother was not present. The young were able to walk by Day 5. On Day 8, for unknown reasons, one of the pups died. Both Ansell (1964) and Dippenaar (1979) previously reported one of the litter dying in the first week of life. Though carrion feeding is well known in *Crocidura* species (Ansell 1964), the mother made no apparent attempt to eat the dead young. By Day 12 the body of the surviving youngster was totally furred but the eyes were still closed. Eye movement and eyeslits were detectable on Day 14. The eyes were fully opened by Day 17 and the activity of the youngster increased tremendously with much exploration and following of the mother.

Throughout this period, caravanning, (Meester 1963; Dippenaar 1979), was not observed but the young did ride on the mother's back. This back riding may have been an aberrant version of caravanning. The mother tolerated riding and suckling attempts until Day 24 when she started to avoid the young. Though she was never aggressive toward the young, the evasive actions suggest the onset of weaning. The youngster was a smaller replica of the adult by the time it was found dead and undamaged in the cage on Day 29.

The mass of the young doubled during the first five days, but declined by approximately 10% over Days 6 and 7 (Table 1). On Day 8, the smaller of the two young (B) died. Subsequently, the surviving young (A) began a steady but slower mass increase. The second mass decrease came just after the eyes were fully open and the young was noted to be extremely active. Mass again decreased after Day 24. This mass loss in conjunction with the observed behavioural changes in the mother again suggest the onset of weaning. Death at 29 days may have been caused by starvation if the young was maladjusting to the weaning as the mass loss indicates. The post-mortem mass was 0,9 g, 88% of its mass on Day 5. The mass of the mother varied between 2,7 and 3,5 g during the post-natal period, a body mass fluctuation of about 20%.

A comparison of the three published observations on *C. bicolor* post-natal development is presented in Table 2. The considerable range in development rates is immediately obvious. Our observations recorded the longest development times while Ansell (1964) recorded the shortest. Three possible

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Table 1 Physical and behavioural development of *Crocidura bicolor* young

Day	Young	Mass (g)	Head-body length (mm)	Head (mm)	Tail (mm)	Behavioural and physical achievements
0	A	$0,25^{a}$	18,7	*	*	naked; eyes and ears closed; movement uncoordinated; soft squeaking
	B	$0,25^{a}$	18,7	*	*	
2	A	$0,50^{a}$	23,8	*	7	unsteady crawling/walking; nipple clinging/ ?caravanning
	B	$0,50^{a}$	24,0	*	5	
5	A	$1,05^{b,c}$	29,55	13,8	11,15	skin turning greyish; walking
	B	$1,0^{b,c}$	28,6	12,95	10,55	
7	A	0,95	33,0	13,95	11,2	hairs becoming visible
	B	0,90	32,1	14,0	11,6	
8	B	0,90	32,5	14,2	11,45	died
10	A	1,0	33,2	14,8	11,75	back riding observed
12	A	1,05	34,0	15,35	12,8	body totally furred; eyes closed
14	A	1,10	34,3	15,6	12,3	tiny eye slits visible; eye movement detectable
17	A	1,15	37,8	18,2	14,4	eyes open; still suckling but playing with insect food
20	A	1,05	**	**	**	extremely active; ears emerging
24	A	1,20	**	**	**	mother resisting back riding
27	A	1,15	**	**	**	ears fully extended; attacking insect food; still attempting to suckle
29	A	0,90				died

^{a} – measurement on a 100 g Pesola spring balance; ^{b} – stomachs full of milk; ^{c} – all further mass measurements taken on a triple-beam balance; * – measurements not taken for fear of injuring young; ** – measurements imprecise due to extremely active young

Table 2 A comparison of some post-natal development times (in days) recorded for *Crocidura bicolor* young in this study, by Dippenaar (1979) and by Ansell (1964)

	This study	Dippenaar	Ansell
Location	Kruger Park, S.A.	Groblersdal, S.A.	Kabompo, Zambia
Habitat	Lowveld	Midveld	?
Litter size	2	4	3
Physical development			
hair appearance	9	6 – 7	6
hair completion	12	10	8
opening of eyes	16	12	10
opening of ears	20	13	11
walking	4 – 5	3	6 – 7
Behavioural development			
duration of caravanning	?2 – 23	3 – 19	7 – 14
interest in solid food	17	19	14
weaning	23 – 27	?	18
active exploration	17	17	11

factors may account for the slower rates we observed. Firstly, the nutritional status of the three females may have been quite different. This could have resulted from the differential diets while in captivity and/or the condition of the females during gestation and at the time of capture. The Satara female was captured during a very severe and prolonged drought when the environmental conditions and food resources were probably very low. Secondly, the three females were from different geographical locations, the Transvaal lowveld and the Transvaal midveld, which are separated by the great escarpment, and Kabompa, Zambia. The differences in development rates shown here may reflect the normal variation for the species throughout its range or alternatively, they may be indicative of geographical variation within the species. Thirdly, the female from the Lowveld was probably substantially smaller than the other two. Unfortunately neither Dippenaar (1979) nor Ansell (1964) reported the original weight or size of their females. However, Dippenaar (*in litt.*) reported that the Satara female's cranial measurements fell just within or below the observed range of variation for the smallest of the southern African *Crocidura* species. This supports Meester's (1963) contention that the lowveld specimens tend to be smaller than other *C. bicolor* from elsewhere in southern Africa. R. Baxter (in Dippenaar 1979) has already suggested that, 'the young of larger females, which tend to produce more milk, grow at a faster rate and that behavioural and physical changes occur earlier in these young than in litters produced by smaller females'.

The fact that this paper, which reports on only a single incident of *C. bicolor* capture, birth and post-natal development, contains previously unknown information, highlights the paucity of knowledge of this species. The tiny musk shrew is noted as occurring in areas of good grass cover and/or where there is vegetation debris (Rautenbach 1982; Smithers 1983). Meester (1963) suggests a distributional correlation with ≥ 500 mm annual rainfall. The *C. bicolor* captures near Satara, which lies between the 500 and 550 mm annual rainfall isohyte (Gertenbach 1980), are consistent with

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Estimation of percentage grass canopy cover and its prediction by regression from biomass data.

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ABSTRACT

The divided disc method is proposed as a new technique for estimating percentage grass canopy cover. The method is validated by comparison of independent cover estimates of the same sites using this method and the wheel point method. Regression analysis was used on the arcsine transformed data. The resultant equation, $y=-2.89+1.03x$; $r^2=.88$, shows close agreement between the two sets of results. Used in conjunction with the disc pasture meter, the divided disc method allows the simultaneous recording of canopy cover and grass biomass data. Field time is greatly reduced and the method is equally applicable at the micro and macro habitat levels.

The environmental variables grass biomass (g/m^2) and grass canopy cover (%) were examined in two habitat types using the disc pasture meter and the divided disc methods. A linear relationship is shown to exist between the two variables. The derived equations are all highly significant ($P<.001$). The equations are compared using analysis of covariance and Tukey's multiple comparisons tests. The common regression equation $y=9.01+.11x$; $r^2=.81$ is accepted as an accurate predictive model of the grass biomass/canopy cover relationship in this study. The use of such a predictive model offers further reduction in field time expenditure.

KEY WORDS: disc pasture meter; divided disc method; grass biomass estimation; percentage grass canopy cover; grasslands; Kruger National Park; point intercept techniques; predictive linear regression; wheel point method

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INTRODUCTION

For most ecological studies, there are innumerable environmental factors which could or should be monitored. The aim of the researcher is to achieve the most comprehensive study with the greatest accuracy and the least expenditure of money, energy and time. This invariably results in a limitation of the number of factors that can be monitored and/or a compromise in accuracy. Any new environmental sampling technique which overcomes some of these compromises is extremely valuable. Similarly beneficial is any consistent and predictive relationship which is found between variables.

The two environmental variables investigated in this paper are grass biomass (g/m^2) and grass cover (%). Both variables have important implications in wildlife ecology. Biomass is often considered a measurement of food availability or utilization whereas cover has a structural emphasis that relates to protection from predators and weather conditions (Gysel & Lyon 1980).

Accurate measurements of grass biomass are often time consuming and labor intensive. Subjective evaluation offers a quick estimate but is difficult to compare between studies due to variation in the skill and effort of the observer. Quantitative estimates can be obtained using a variety of techniques. The clip quadrat is a commonly used method (Getz 1961a,b, Goertz 1964, Birney _et al_ 1976). Although accurate, it is habitat destructive and highly labor intensive. Other biomass techniques include weight estimation (Hutchings & Schmautz 1969, Anderson & Kothmann 1982), visual obstruction (Robel _et al_ 1970) and electronic capacitance (Neal & Neal 1973). The relatively new disc pasture meter method utilized by Bransby _et al_ (1977) and Bransby & Tainton (1977) offers a rapid and easy method of grass biomass estimation that is also non-habitat destructive.

Quantitative cover measurements usually require altogether different techniques such as point-intercept (Evans & Love 1957, Kern 1981), sampling frame (Daubenmire & Daubenmire 1968), line intercept (Canfield 1941, Goertz 1964) or chart quadrat (Mueller-Dombois & Ellenberg 1974). All of these need different equipment

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from that used for grass biomass estimation and subsequently increase time by requiring additional measurements.

A linear relationship between plant biomass and canopy cover has long been recognized (Cook et al 1948) and appreciated for its time saving qualities. Inverse prediction from regression has been used at the species-specific level to obtain biomass estimates for woody vegetation (Bentley et al 1970) and herbaceous vegetation (Payne 1974, Humphrey 1985) from absolute canopy cover. The relationship between relative canopy cover (%) and grass biomass has not been investigated either at the species -specific level or for the grass community as a whole.

In this paper, I describe a quantitative cover estimation technique, the divided disc method, which can be used in conjunction with the disc pasture meter. It allows simultaneous recording of data for grass biomass and percentage canopy cover. The method is validated by comparisons with results from the wheel point method, a point-intercept technique. I then examine the relationship between grass biomass and relative canopy cover. Results obtained under varying habitat and environmental conditions are compared to examine the consistency of the relationships. Although the examination of the relationship between grass biomass and relative grass canopy cover was part of a small mammal study, the methods described can be applied to other ecological studies after appropriate modification.

METHODS

The data for this study were obtained during a two-year small mammal ecology project in the central region of the Kruger National Park, South Africa. The two habitats under study were physiognomically quite different. Habitat 1 was a uniform grassland with a few scattered large trees. Habitat 2 had interspersed patches of open ground, grassland and woodland. Clear differences in the structural heterogeneity, grass species, and the extent and uniformity of the grass layer were apparent between the two habitats. Two small mammal trapping sites in each habitat were monitored. Each site consisted of two parallel lines approximately 1km long and 50m apart with a 20m trap

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spacing. This resulted in the monitoring of approximately 43 contiguous plots per line. Plot sizes of 20m X 20m were used, based on the need for assessment of the microhabitat surrounding each small mammal trap.

The disc pasture meter method (Bransby & Tainton 1977) was chosen to measure grass biomass for its simple and non-destructive properties. Assessed as reliable and accurate in a variety of field situations (Danckwerts & Trollope 1980, Hardy & Mentis 1985), it is now being used in numerous other studies (Trollope 1983, Trollope & Potgieter 1985, 1986, Dewit pers. comm., Bowland pers. comm.). The disc pasture meter consists of a central rod with calibrated centimetre intervals marked on it, and a known mass disc with sleeve (1.5kg and 458mm diameter) (Fig. 1). The disc and sleeve are raised to the top of the central rod and then dropped. The disc settles on the grass layer below it and the settling height is then read in centimetres. This method relies on a linear relationship between disc settling height and the grass biomass beneath it. Calibration and establishment of the exact linear equation to be used must be done for different field situations. This procedure was performed by Trollope & Potgieter (1986) for grass conditions in the central Kruger National Park. The equation $y=-3019+2260\sqrt{\bar{x}}$ ($r^2=.90$), where $\bar{x}$ is the mean settling height of the disc (cm) and y is the grass biomass estimate (kg/ha), was derived.

For this study, a grass biomass estimate in kg/ha was impractical for the small plot sizes (20m X 20m or 0.04ha) used so the equation was scaled down by a factor of 10 to produce a result in g/m^2. Based on the a priori reasoning that the grass biomass estimate should be accurate at a level greater than that which may have a biological influence on small mammals, a level of precision no less than $75g/m^2$ was decided on. Using the standard equation for calculating the confidence bands around the regression equation (Zar 1984) for the results of the original calibration process (Trollope & Potgeiter 1986) an appropriate sample size (No. of disc height readings) necessary for the desired level of precision was estimated iteratively. This procedure showed that a sample size of 12 disc readings was

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sufficient to maintain a precision level of 75g/m^2 or greater at the 95% confidence limits over a large range of disc heights. The range of the confidence bands for a sample size of 12 varied from 18±63g/m^2 at 2cm and 376±56g/m^2 at 9cm to 956±73g/m^2 at 31cm. The mean disc heights obtained in this study ranged between 1.8 and 17cm, giving a biomass range of 0 to 630g/m^2, well within the range of the original calibration data.

Within each plot, a reading was taken every three strides on two perpendicularly bisecting diagonal axes (Fig. 2b). The mean settling height of the 12 readings was then used in the equation $y=-301.9+226\sqrt{\bar{x}}$. If the disc fell on woody vegetation, a sidestep toward the center of the plot (thus measuring the grass closer to rather than farther from the point of small mammal capture) was taken until the woody vegetation was avoided. When this situation arose, usually no more than one or two sidesteps were ever required.

Two methods for percentage grass canopy cover were used. The divided disc method was developed for use with the disc pasture meter to economize on time and equipment and to allow reliable grass cover estimates to be made on the small plots. To determine cover, I marked (using masking tape) the disc portion of the disc pasture meter into 8 equal segments (Fig.1). When the disc was dropped, the settling height was taken and each segment that had enough grass protruding along its edge to obscure from view more than half the ground beneath it, was counted. Percentage grass cover for the entire plot was calculated as No. covered sections / total sections available X 100. The total number of sections available per plot was 96 (i.e. 8 sections X 12 readings).

The divided disc results were validated by comparison with results from the wheel point method, (Mentis 1981, Kern 1981). This method involves pushing a large wheel, (diameter about 700mm) which has two color marked spokes, through the grass. When the marked spokes touch ground, the presence or absence of cover at that point is recorded. A botanist regards this procedure as a method for determining plant basal cover (Mentis 1981) but, in the case of small mammals, cover, be it aerial or basal, is the important criteria. Thus, if the spoke was hidden

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from view in any way, it was counted as cover present. Percentage cover is then calculated as cover strikes / total marked spoke strikes X 100. For a reliable estimate, this method requires a large number of strike counts per area (Potgieter pers. comm.). Kern (1981) used 1000 points for 3.2ha plots. As the circumference of the wheel (2.2m) obtained from the Kruger Park research division was too large to be used reliably on 20m X 20m plots, four consecutive plots were considered as one. Five parallel lines were followed in each group of plots which generated approximately 350 points per 0.16ha (Fig. 2a) or 2188 points/ha. The divided disc results for the same plots were then averaged and used as the comparative data. Data were taken over as wide a range of cover situations (14% to 89%) as possible. Percent cover estimates were arcsine transformed for comparison using linear regression analysis. If the two methods actually yield the same cover estimates, the slope of the regression should be equal to (or very close to) 1.0 and the back transformed y-intercept should lie near the origin.

Data for the grass biomass and percentage canopy cover were taken during dry and wet seasons in the two habitats. The relationship between them was examined using linear regression. Regression equations were compared using analysis of covariance with Tukey's multiple comparisons tests (Zar 1984).

RESULTS

The relationship between the cover estimates produced by the divided disc and wheel point methods, as described by the equation $y=-2.89+1.03x$; $r^2=.88$ (Fig. 3), is highly significant ($P<.001$). The slope is virtually 1.0 (1.03 ± 0.07) showing a one to one change relationship in cover estimates. By back transforming the -2.89^0 elevation to percent cover, the y-intercept is .26% which is essentially through the origin. Therefore, the two criteria set out in the methods section are satisfied and the equality of the two methods can be accepted with confidence.

Linear regressions of grass biomass and canopy cover for dry and wet season conditions in the two habitats are summarized in Table 1. The slopes of these regressions are all very similar

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and highly significant ($P<.001$). To determine whether the equations derived in each habitat were describing the same general relationship, analysis of covariance was performed on each habitat's combined data. These analyses revealed no significant heterogeneity among the slopes from either habitat although, heterogeneity among the elevations ($P<.001$) was apparent (Table 2). The application of Tukey's multiple comparisons tests failed to reveal any deviant elevations in either habitat, thus showing an even distribution in the heterogeneity.

The variation in elevations, when back transformed to percentage cover, ranged from .8% to 4.5% in habitat 1 and 1.4% to 3.8% in habitat 2 (Table 1). This is a net difference of 3.7 and 2.4% respectively. The minimum detectable difference in the grass biomass estimate was $75g/m^2$ ($P<.05$) which results in a variation potential of 8% for the cover estimates. Thus, the potential variability of the elevations within the accuracy limit set for the grass biomass estimates is greater than the potential 4% elevation heterogeneity found in the cover estimates. Therefore, despite the statistically significant difference in the arcsine transformed elevations, the equations derived in each habitat are accepted as equivalent and the common equations are accepted as the best fit regressions lines.

The common regression equations for habitats 1 and 2 are very close. Analysis of covariance on all eight lines generated the common regression equation $y=9.01+.11x$; $r^2 =.81$ (Table 2). Heterogeneity among the elevations is again apparent but as the range of slopes and elevations in Habitat 2 are encompassed by those in Habitat 1, there is no change in the potential level of variation so, as before, they are within the accuracy limits of the grass biomass estimate. This equation is accepted as an accurate model of the relationship between grass biomass and canopy cover in this study area.

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DISCUSSION

Previous assessment studies of the disc pasture meter have shown its effectiveness in estimating grass biomass (Danckwerts & Trollope 1980, Hardy & Mentis 1985). The results from this study have shown that the divided disc method gives reliable and accurate percentage canopy cover estimates over a wide range of cover situations. The combination of these two methods reduces some of the problems mentioned in the Introduction, since only one instrument is needed and two variables can be recorded simultaneously. In addition, the methods have the advantage of causing minimum disturbance of the habitat and enable repeated observations to be made at the same study site. Though an initial calibration procedure is necessary for valid use of the disc pasture meter, once done, these methods can be used at the macrohabitat level (Danckwerts & Trollope 1980, Trollope & Potgieter 1985, 1986) or the microhabitat level by choosing appropriate plot sizes. The sample size needed for the desired level of significance can then be calculated.

The linear relationship between grass biomass and percentage canopy cover in this study was remarkably consistent. Data were obtained in extremes of environmental conditions and in two different habitats, yet the resulting slopes of the regression equations were nearly identical. This shows a consistency and strength in the relationship which transcends variations in habitat and environmental conditions. The heterogeneity in the elevations was shown to lie within the accuracy limits expected in the grass biomass estimates and so were accepted as non-significant for this study. Though the accuracy of the biomass estimate could be refined, the additional expenditure and the real biological relevancy or usefulness of such accuracy, at least for small mammals, are questionable.

It is important that the consistency of this relationship is assessed in other field situations. The investigation and establishment of a linear relationship between grass biomass and canopy cover again reduces field time as it requires the recording of only one variable for the effective monitoring of two important environmental factors.

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ACKNOWLEDGEMENTS

This project was financed by the Mammal Research Institute, University of Pretoria and the S.A. Council for Scientific and Industrial Research. I am grateful to the National Parks Board for allowing me to carry out this work in the Kruger Park. I am very thankful to W. Trollope and A. Potgieter for introducing me to the disc pasture meter and to I. Henschel for helping with the fieldwork using the wheel-point apparatus. I am grateful to R. Pietruszka for his statistical advice and to R. Watson for his help and advice throughout the entire study. My thanks to R. Watson, W. Trollope, D. Kelso, J. Rasmussen, C. Crawford, R. Pietruszka and H. Dott for their helpful comments on earlier manuscripts.

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Table 1: Comparison of the regression equations for grass biomass (x) (g/m^2) and arcsine transformed percentage grass canopy cover (y) (°) in two habitats during dry and wet season conditions. * = P .001.

Habitat 1	Season	n	Regression equations (r^2)	F-ratio (df)	Back-transformed y-intercept (%)
1	dry	86	$y=4.95+.13x$ (.66)	161.3 (1,84)*	0.8
2	dry	90	$y=11.76+.12x$ (.81)	365.5 (1,88)*	4.1
3	wet	84	$y=12.31+.10x$ (.59)	117.7 (1,82)*	4.5
4	wet	84	$y=12.34+.11x$ (.79)	307.3 (1,82)*	4.5
Habitat 2					
1	dry	88	$y=7.42+.12x$ (.89)	702.6 (1,86)*	1.7
2	dry	90	$y=6.70+.12x$ (.79)	332.9 (1,88)*	1.4
3	wet	81	$y=7.85+.11x$ (.92)	949.5 (1,79)*	1.9
4	wet	84	$y=11.24+.12x$ (.91)	847.9 (1,82)*	3.8

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Table 2: Common regression equations for habitats 1,2 and the combined habitats as derived from analysis of covariance (x = grass biomass (g/m^2); y = arcsine transformed percentage grass canopy cover (°)). * = P .001.

Habitat	Common regression (r^2)	F-ratio Heterogeneity of slopes (df)	F-ratio Heterogeneity of elevations (df)	Back-transformed y-intercept (%)
1	$y=10.21+.11x$ (.74)	1.15 (3,336)	20.21 (3,339)*	3.1
2	$y=8.45+.11x$ (.88)	1.06 (3,335)	17.75 (3,338)*	2.2
1+2	$y=9.01+.11x$ (.81)	1.08 (7,761)	16.49 (7,678)*	2.5

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Figure Headings:

Figure 1: Schematic diagram of the disc pasture meter with the eight equal segments marked for the divided disc cover estimation. (for construction details of the disc pasture meter see Bransby and Tainton 1977).

Figure 2: Patterns for data collection A) transects followed for percentage grass canopy cover estimation using the wheel-point method. B) transects followed for grass biomass and grass canopy cover estimation using the disc pasture meter.

Figure 3: Linear regression of arcsine transformed percentage cover data obtained from both the divided disc and wheel-point methods.

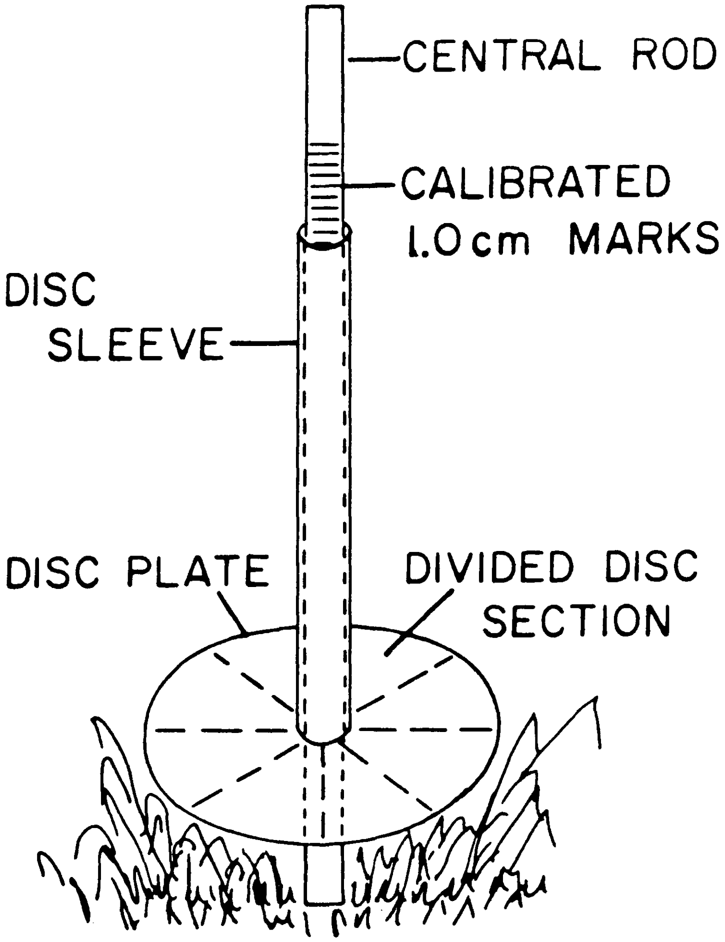

Figure 1

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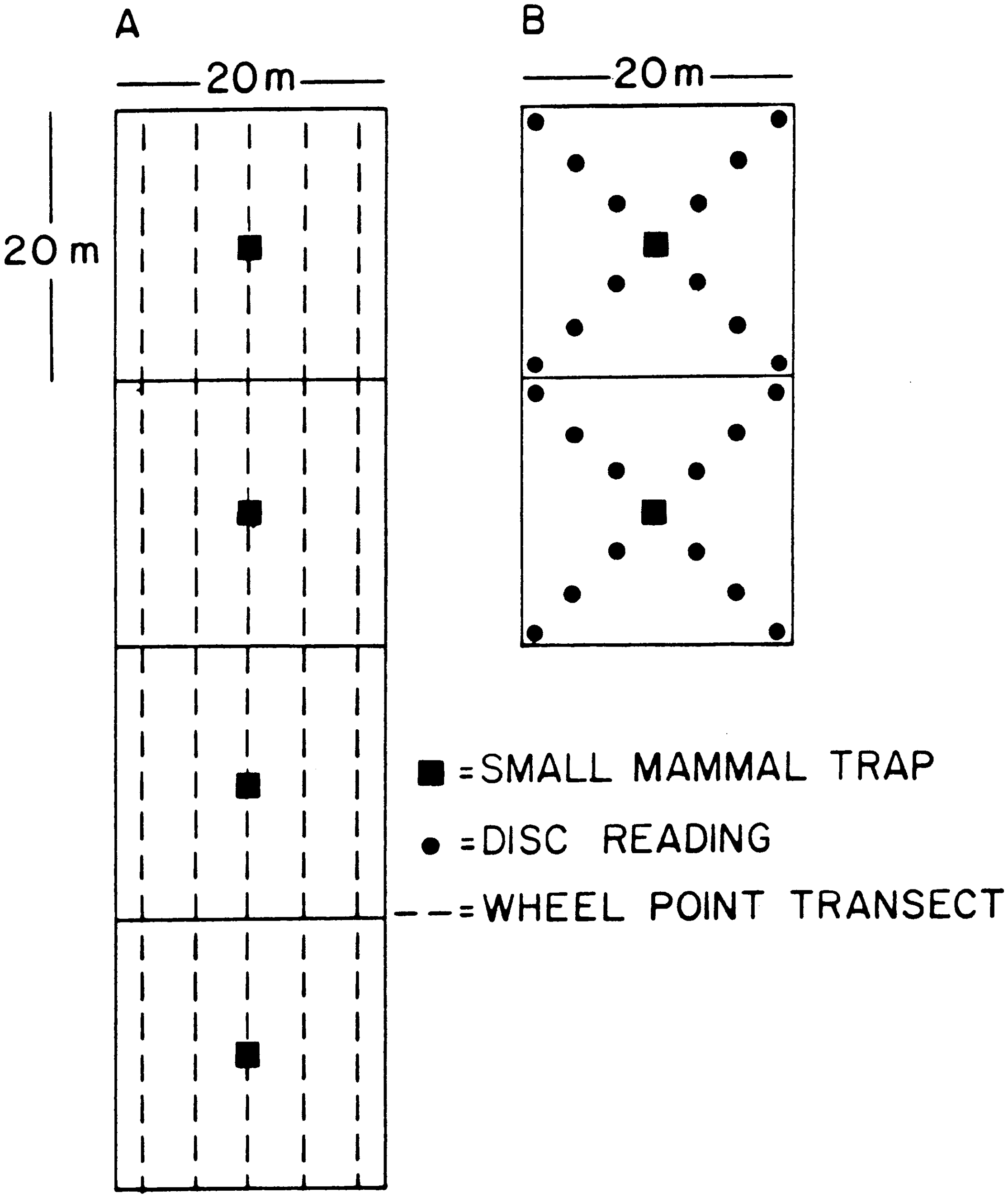

Figure 2

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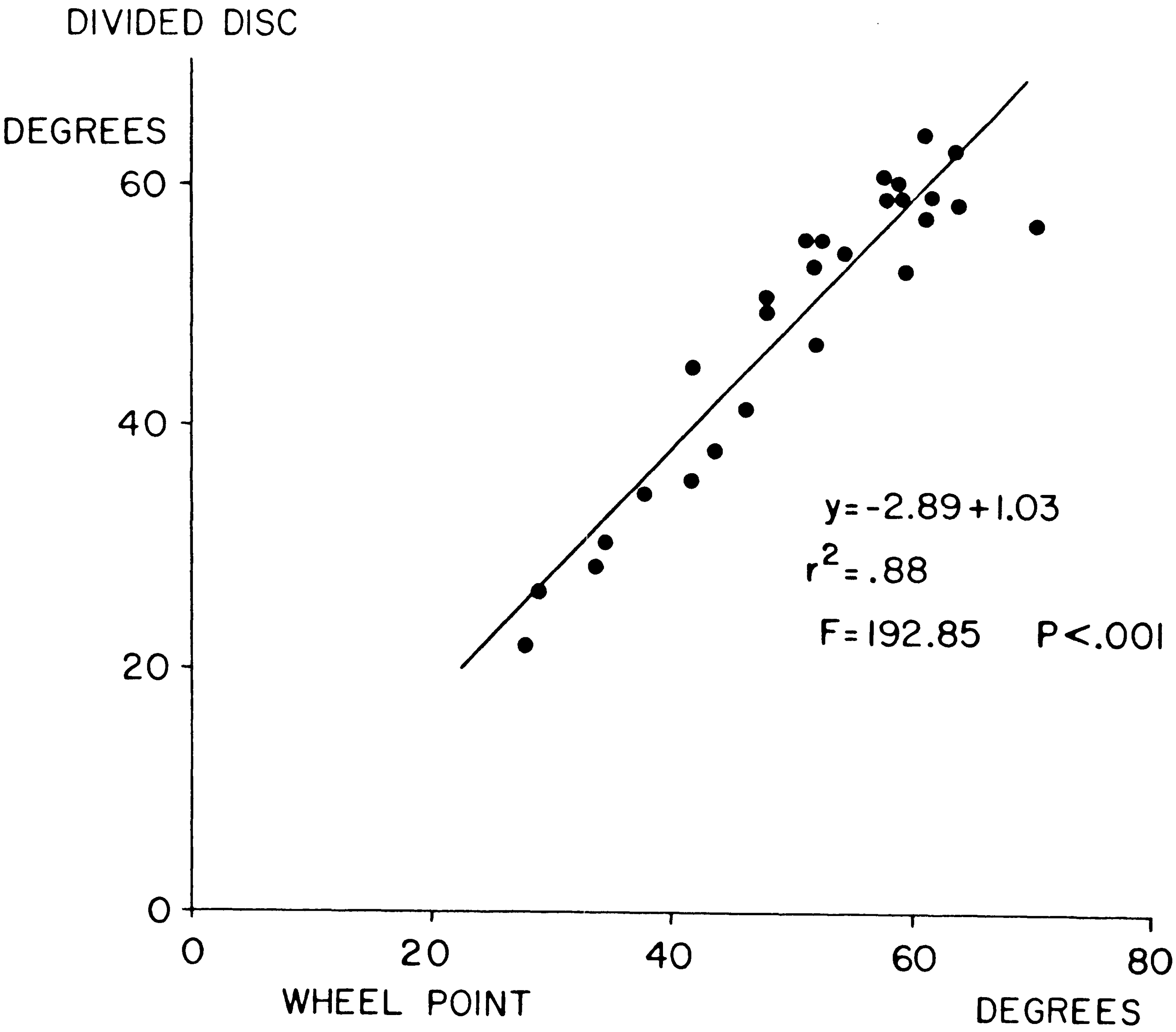

Figure 3

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