M. R. BORTHWICK

HABITAT USE
BY THE WHITE RHINOCEROS
IN PILANESBERG GAME RESERVE

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HABITAT USE BY THE WHITE RHINOCEROS IN RELATION TO OTHER GRAZING UNGULATES IN PILANESBERG GAME RESERVE, BOPHUTHATSWANA.

Michael Robert Borthwick

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DECLARATION

I declare that this dissertation is all the work of

Michael Robert BORTHWICK.

It is being submitted posthumously for the degree of Master of Science in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other university.

Dr R.N. Owen-Smith (Supervisor)

27th day of March, 1986.

HABITAT USE BY THE WHITE RHINOCEROS IN RELATION TO OTHER GRAZING UNGULATES IN PILANESBERG NATIONAL PARK, BOPHUTHATSWANA

MICHAEL ROBERT BORTHWICK

ABSTRACT

This study investigated resource use by the white rhinoceros (Ceratotherium simum) as a basis for assessing the carrying capacity for this species in Pilanesberg Game Reserve, Bophuthatswana. The resources considered included (i) habitat types, and (ii) food in terms of grassland structures. Their use by white rhinos was analysed in relation to resource use by other grazing ungulates.

White rhinos favoured secondary grasslands during the wet season, and wooded valley savanna and thicket during the dry season. Shorter grassland was generally favoured, except during the late dry season. Habitat selection became more broad after fire. Correspondence analysis confirmed tree canopy cover and grass height as the major factors in vegetation type selection.

Discriminant function analysis showed that wildebeest overlapped most with white rhino in their habitat use, and zebra least. Dietary overlap during the dry season was also high between white rhino and wildebeest. Total niche overlap considering both habitat and diet was considerably less than indicated on either single resource axis.

Two standard methods and modifications thereof for assessing carrying capacity were applied: (i) relation between ungulate metabolic biomass and rainfall; (ii) assessments of agricultural stocking density. Shortcomings were identified. A novel "weighted consumption" model for assessing carrying capacity was developed. This model highlighted a need for further information on minimum grazing thresholds for different grassland types.

TABLE OF CONTENTS

CHAPTER PAGE

1 INTRODUCTION

2 THE STUDY AREA

3 THE AVAILABLE RESOURCES

4 HABITAT AND FOOD SELECTION BY GRAZING UNGULATES AT PILANESBERG

5 HABITAT AND DIETARY OVERLAP BETWEEN THE PILANESBERG GRAZERS

5.2 Methods

6 MEASUREMENT OF CARRYING CAPACITY IN A MULTISPECIES SYSTEM

CHAPTER ONE

INTRODUCTION

1.1 Background to Study

In the face of increasing pressures from human expansion and urbanization, the long term survival of many species and communities depends on their protection within fenced boundaries. Invariably, these areas are smaller than the original ranges of at least some of the species they contain, and consequently prevent herbivore migration in response to increasing population and habitat deterioration. Most reserves in southern Africa are small (less than 500 sq. km, East 1981), thus restricting the free movement of herbivores to a limited choice of habitats. These seasonal migratory habits allow for the dispersal of herbivores between their wet season and dry season ranges. For instance, Maddock (1979) found that wildebeest, zebra and Thomson's gazelle all migrate between their wet season range on the open plains and their dry season range in the woodlands. He concluded that both food and water availability (and indirectly rainfall) were the major factors influencing their annual movements.

A severing of the herbivores' dispersal patterns could lead to a reduction in the ability of the reserves to support the high densities which were originally present (Maddock, 1975, 1979; Western, 1975). Berry and Siegfried (1979) showed that a marked downward trend occurred in the wildebeest (Connochaetes taurinus) population of the Etosha National Park after their seasonal migration routes were prevented by a boundary fence. Western (1975) estimates that if the seasonal migration of herbivores in the Amboseli Nature Reserve (3000 sq. km) in southern Kenya were severed, it would lead to a 30% reduction in biomass. The herbivores would now have to forage in habitats which were previously avoided.

Long distance dispersal such as migration, is of course not the only type of movement prevented by boundary fences, movement from one habitat or valley to another is of equal importance. This type of movement involves all animals irrespective of whether they are migrants or not. Owen-Smith (1981) stressed the importance of herbivore management, in terms of white rhino removals, in the Umfolozi-Corridor-Hluhluwe Game Reserve Complex. With the construction of a rhino proof fence, dispersal into the surrounding less productive areas was prevented. This has consequently led to an overabundance of white rhinos in the reserve and a rapid overutilization of their habitat. Thus the ability to assess the affects of boundaries on herbivore feeding ecology is an important prerequisite for sound management both on the short- and long-term basis.

The Pilanesberg Game Reserve in Bophuthatswana (53500 ha) is a typical example of such an "island" reserve. It was proclaimed in 1979 in an old agricultural area. One of the major questions facing management is how many animals and which species should be stocked. In particular, the number of white rhinoceroses (Ceratotherium simum) is crucial firstly, because they are most valuable economically and, secondly, in their capacity as "megaherbivores" (Owen-Smith, 1981), they are most capable of modifying the vegetation. It was these problems which led to the development of this project.

The problem of small game reserves is compounded by the fact that they are based on arbitrary or political rather than natural boundaries. The Pilanesberg Game Reserve is situated in the crater of an extinct volcano and because of its generally hilly topography and alkaline soils the vegetation is relatively less productive than the surrounding flat "sweet-veld" areas (Tinley, 1978). Based on verbal accounts (Tinley, 1978) most of the herbivores present in the reserve today used the crater as a marginal habitat possibly during the drier periods. Consequently, with the construction of the boundary fence and the rapid urbanization of the surrounding areas, local seasonal movements between habitats was prevented, hence lowering the potential carrying capacity of the reserve. In addition, prior to its establishment much of the reserve, especially the more productive valleys were divided into a number of farms on which cultivation and cattle farming were practised. Since their abandonment, these areas have developed into secondary grasslands and thickets of various successional stages. Consequently, man's presence over the years has altered the natural state of these habitats, necessitating a need for an understanding of these modified areas in relation to herbivore selection and distribution (Vernede, 1983).

1.1.1 Carrying Capacity

Meissner (1982) expressed the importance of the concept "carrying capacity" as a prerequisite for the development of sound management systems, planning of reserves and their evaluation in terms of secondary production, particularly those involving multiple species. Theoretically this may be sound, but when applied practically it leads to confusion giving rise to a number of problems.

The distinction between the "economic" and the "ecological" carrying capacities has caused conceptual difficulties and misunderstandings (Caughley, 1976, 1981) especially between wildlife managers and agriculturalists. The ecological carrying capacity is defined as the "number or biomass of animals which come into equilibrium with the vegetation" (Caughley, 1976). In this case there is no need to estimate carrying capacity numbers, since the ecological carrying capacity is simply that number of animals that will be there when the numbers have stopped changing. However, if one is interested in the economic or grazing carrying capacity, i.e. the stocking density at which the net yield in animal biomass is at a maximum (Caughley, 1976), then the animal numbers must be monitored in order to predict this density.

The second difficulty when applying this concept lies in the accuracy of calculating the carrying capacity density. Being complex and dynamic, it necessitates the simultaneous inclusion of ecological factors such as interseasonal variation, spatial variability within the community, plant species composition, interactions between plants and herbivores, seasonal changes in plant food value, and interactions between the herbivores. If simplified, two main aspects of a plant-herbivore system must be recognized, namely, the availability of the resources and the animal requirements, whether in terms of protein or energy. It must be stressed that the numerical calculation of carrying capacity on a long-term basis becomes far more complex when the inclusion of environmental fluctuations and time lag effects are included. In response to these difficulties, Moen (1973) concluded that the idea of carrying capacity is best approached as a concept rather than as a simple, definable entity. A more extensive literature review of the concept of carrying capacity is presented in chapter six.

Attempts to develop objective approaches in estimating carrying capacity numbers have been largely confined to agricultural livestock on which considerable emphasis is placed on experience and guesswork. This problem is compounded when considering a multispecies wildlife system in which different interactive effects on the vegetation by the herbivore species is apparent. The estimation of carrying capacity and the subsequent management of nature reserves or cattle ranches should therefore be based on analyses at the community or ecosystem level. Analyses of this nature cannot be focussed on single species independent of their interactions. It is the mechanisms which regulate both the plant and animal densities which are important.

1.1.2 Resource Use

Estimating carrying capacity numbers essentially involves an analysis of the use of resources within the ecosystem or community. Resource use can be influenced by two important factors, namely, the availabilty of the resource type and the selection for those resources (eg. habitat and food) by the animals. The pattern of resource use may of course be affected by other coexisting consumers. Hence, consumer interactions should also be analyzed.

Two major processes or mechanisms which are believed to contribute to the patterning of resource allocations among species, and their spatial and temporal abundances, are competition and predation (Schoener, 1974). Connell (1975) maintained that although the distribution and abundance of species (e.g. barnacles) are ultimately determined by their tolerances to extremes of physical conditions, smaller differences result from interactions with other organisms. The two interspecific interactions occur either between trophic levels, i.e. predation, or within trophic levels, i.e. competition. Consequently, the extent of both competition and predation should influence the carrying capacity of a predator-prey or plant-herbivore system.

Niche packing, niche overlap and the factors governing both niche breadth and shape are all important factors in the determination of community structure and resource partitioning (Thomson and Rusterholz, 1982; Hanski, 1978; Lawlor, 1980). Various models have shown that the presence of a competitor reduces the equilibrium number of a species (e.g. Rosenzweig, 1979). The determination of the degree of niche overlap between species should allow for a better understanding of the extent of the interactions. Consequently, a knowledge of the niche metrics within a community would provide valuable information for estimating combined carrying capacities with respect to various mixtures of the two species.

Food supply, being an important parameter in regulating the population size of herbivores, should therefore provide insight into the basic principles governing the structure of ecosystems. Duncan (1975) maintained that the extent of utilization of the various components is greatly influenced by interspecific competition between predators (or herbivores). This again emphasizes the need for analysing dietary niche overlap within multispecies systems. Chapter five discusses the theory of niche overlap and its relationship to carrying capacity in more detail.

1.1.3 The White Rhinoceros

To date, only two studies in southern Africa (Owen-Smith, 1973 and Condy, 1973) have been done on the biology of the white rhinoceros. Although greater emphasis was placed on their behavioral ecology, certain aspects of their feeding ecology were noted.

The white rhinoceros is regarded as a short grass grazer (Player and Feely, 1960; Foster, 1967) but generally utilizing the long grass areas during the drier periods or under higher population densities (Owen-Smith, 1973). Thus there appears to be a seasonal shift from regions of lawn-like grasslands to long grass areas, with a greater preference for the former (Owen-Smith, 1973). However, this apparent higher preference for short grasslands may simply be a reflection of the intense grazing pressure exerted by these animals, and hence does not adequately depict their true habitat choice.

Owen-Smith (1973) found that the white rhinos in the Umfolozi Game Reserve favoured the short creeping grasses such as *Urochloa mosambicensis*, *Panicum coloratum*, and *Sporobolus smutsii*. These species are characteristic of a low structural cellulose to cellular content ratio, i.e. highly nutritious. During the drier season however, increasing use is made of the taller grass species , e.g. *Themeda triandra*, *Panicum maximum* and *Digitaria argyrograpta* which have a high structural cellulose to cellular content ratio. The critical condition of these animals is believed to be dependent on the length of time that they have to utilize this submaintenance diet. However, because of their faster rates of food passage these non-ruminants can extract more protein per unit time and can therefore survive better than most ruminants on this fibrous forage (Bell, 1971; Jarman, 1972). Furthermore, because of their lower metabolic rates these animals lose weight relatively more slowly than smaller species and consequently should be able to survive better than their competitors (Owen-Smith, 1973). This relationship between forage choice, body mass and digestive techniques, known as the Bell-Jarman principle (Geist, 1975) has been used to explain the relatively high white rhino biomass in both the Umfolozi Game Reserve (60% of the herbivore biomass - Owen-Smith, 1973; 1981) and the Rwenzori National Park, Uganda (40% of the herbivore biomass - Field and Laws, 1970). White rhinos are therefore an important grazing ungulate to consider when relating herbivore densities to habitat impact.

1.2 Scope and Objectives

Over 250 white rhinos have been introduced into the Pilanesberg Game Reserve over the past four years. This amounts to over 450 000 kg of live grazing biomass out of a total of approximately 1,5 million kg, i.e. just under 30% of the total ungulate biomass is white rhino. However, in terms of stocking density, it represents a density of only 0.75 kg/ha.

The overall objective of this study was to provide an estimate of the numbers of white rhino which the reserve could safely stock, given different combinations of numbers of the other grazing species. The specific objectives required to meet the overall aim were:

(i) To record, on a seasonal basis, the spatial distribution and habitat use of those grazers in the reserve which overlap with the white rhino, i.e. wildebeest (Connochaetes taurinus), hartebeest (Alcelaphus buselapha), zebra (Equus burchelli) and impala (Aepycerus melampus).

(ii) To determine the dietary composition of each of these herbivores in each habitat.

(iii) To analyze those features of the grassland structure and species composition which influence habitat selection.

(iv) To measure the association and degree of overlap in both habitat use and dietary selection between the white rhinos and the other potential competitive grazers.

1.3 Approach

Initially, the major habitats in the reserve were classified according to the plant species composition (bulk contribution) of the herbaceous layer, topography and successional stage.

The diet and habitat selection of the major ungulate grazers was determined, with special emphasis placed on the white rhinoceros. Then, with the knowledge of the relationship between the diet and grassland structure (height, biomasss, and proportion of the different grasses), the degree to which the herbivores select the different grassland types was analyzed. Overlap measures between the white rhino and the associated grazers were then calculated using the selection coefficients determined along both the habitat and dietary niche dimensions (refer to chapter five).

Finally, four different methods of calculating carrying capacity were presented. The first two are the standard methods currently used by agriculturalists based on the relationship between rainfall and maximum supportable herbivore biomass (Coe, et al, 1976). The third and fourth are modifications of the previous two. A model based on a supply and demand approach is presented which analyzes the importance of the "minimum grazing threshold" on carrying capacity assessments.

CHAPTER TWO

THE STUDY AREA

2.1 Location

The Pilanesberg Game Reserve, Bophuthatswana is situated in the Western Bushveld, between latitudes 25 degrees 10 minutes - 25 degrees 20 minutes, south and 26 degrees 5 minutes - 27 degrees 10 minutes, east. The reserve is situated within an extinct volcano, approximately 50km north of Rustenburg, Transvaal. It is approximately 53500 ha in size and is on average 26 km in diameter. A number of cattle and agricultural farms border the reserve. The town Heystekrand borders the eastern boundary.

2.2 Climate

The Pilanesberg Game Reserve occurs within the drier end of the intermediate or mesic biome (Tinley, 1978). The climate, which is typically subtropical has been divided up into three seasons (Tinley, 1978), the hot-wet season extending from November to March and the cooler drier period until July, followed by the hot-dry period from August to October.

The annual rainfall, measured at the Pilanesberg Police Station and Saulspoort Hospital since 1961 (supplied by the weather bureau in Pretoria), is shown in Figure 2.1. The mean annual rainfall for the 22 year period was 620 mm. The 1960's were generally below average, while the 1970's were above average. Severe droughts occurred during the periods, 1962-63, 1964-65 and 1970 and again during the 1981-82 and 1982-83 seasons. In general, the central valley station (Pilanesberg Police Station) some 50m higher in altitude than the peripheral poort station (Saulspoort Hospital) has a lower rainfall.

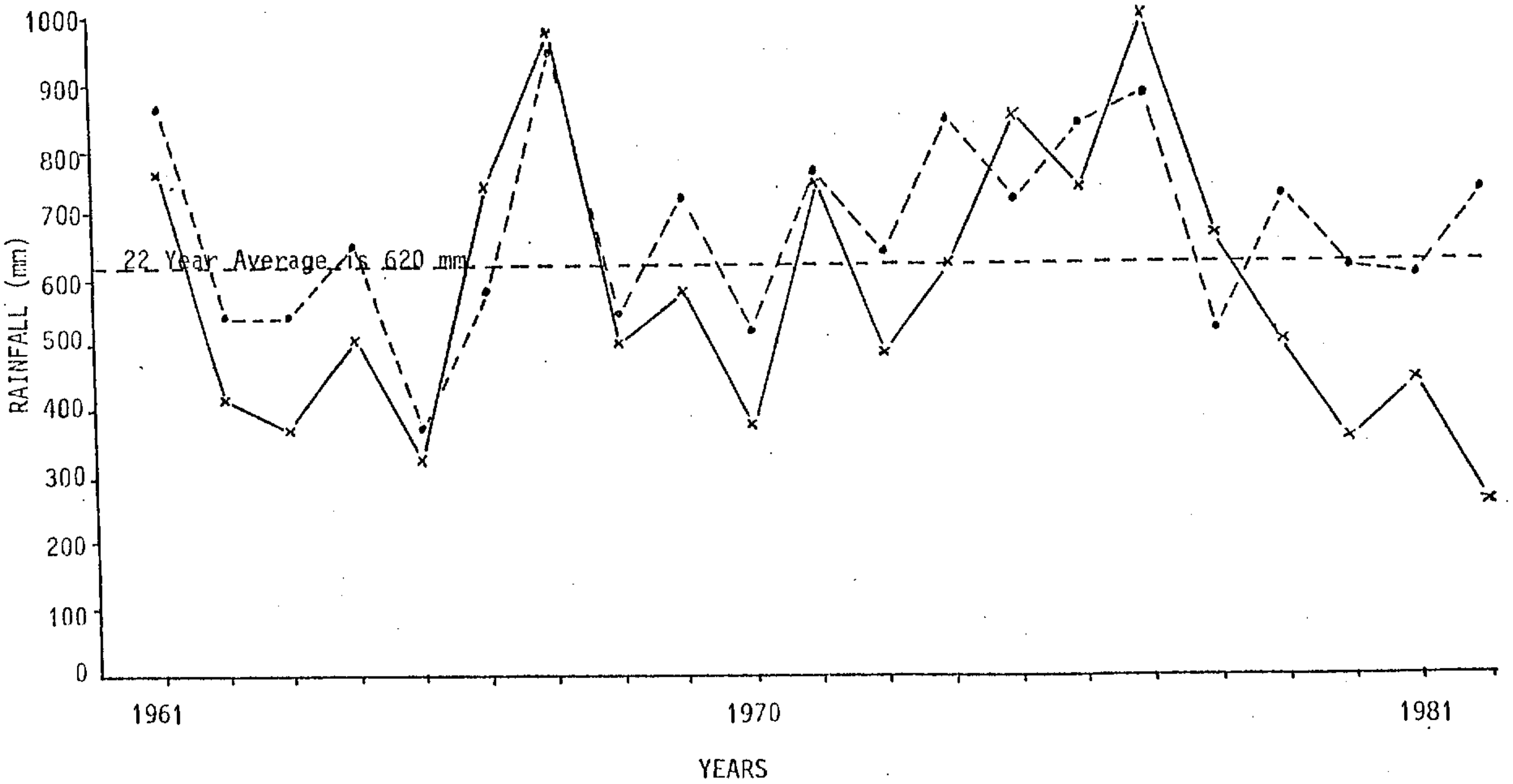


Figure 2.1 : Annual Rainfall over 22 years at two Weather Stations outside the Pilanesberg Game Reserve. (×—× is the Pilanesberg Police Station, 25 15'S, 27 07'E and •--• is the Saulspoort Hospital, 25 10'S, 27 10'E).

Figure 2.2 illustrates the average monthly rainfall figures of the two weather stations, for the 22 year period. December and January are the wetter months with June, July and August being the driest. A comparison of the monthly rainfall during the study period (Figure 2.3) with that of the long-term monthly averages, reveals that a slightly less than average rainfall was experienced.

The highest temperatures were experienced during the summer months which varied between 18 and 20 degrees Centigrade . These high temperatures correspond with the increased rainfall periods, thus leading to an increased humidity (van der Meulen, 1979). The winters are mild and dry with mean temperatures varying from 12 to 18 degrees Centigrade. The annual mean temperature was 18.6 degrees Centigrade (Tinley, 1978).

2.3 **Topography and Geology**

The altitude of the reserve varies between 1160m and 1675m above sea level. Pilanesberg has been described by Tinley (1978) as an "isolated, oval series of concentric hill ranges and valleys composed of a suite of alkaline volcanic rocks" (see Figure 2.4).

The geology of the Pilanesberg system has been divided basically into two main groups (Tinley, 1978);

(i) A cover of alkaline volcanic and pyroclastic rocks, mostly stripped off by erosion leaving isolated patches of alkaline lava tufts and coarse breccias, and

(ii) an intrusive base composed mainly of foyenite and syenite rocks.

The surrounding plains on either side of the volcanic system are formed on red granite to the east, and norite of the Bushveld complex, to the west. For a more detailed description of the geology refer to Truswell (1977).

Generally, the form of the hills was controlled by the intrusive

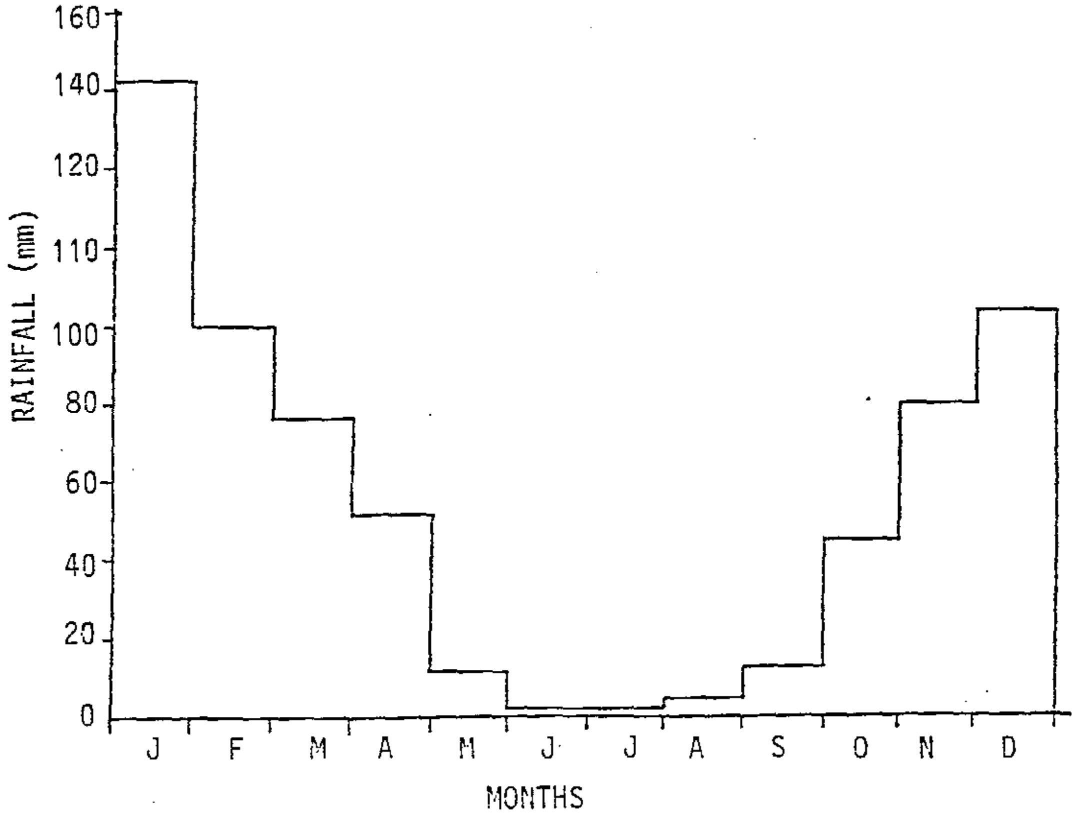


Figure 2.2 : Average Monthly Rainfall at the two Weather Stations, Saulspoort Hospital (25 10' S, 27 10' E) and Pilanesberg Police Station (25 15' S, 27 07' E) outside the Pilanesberg System.

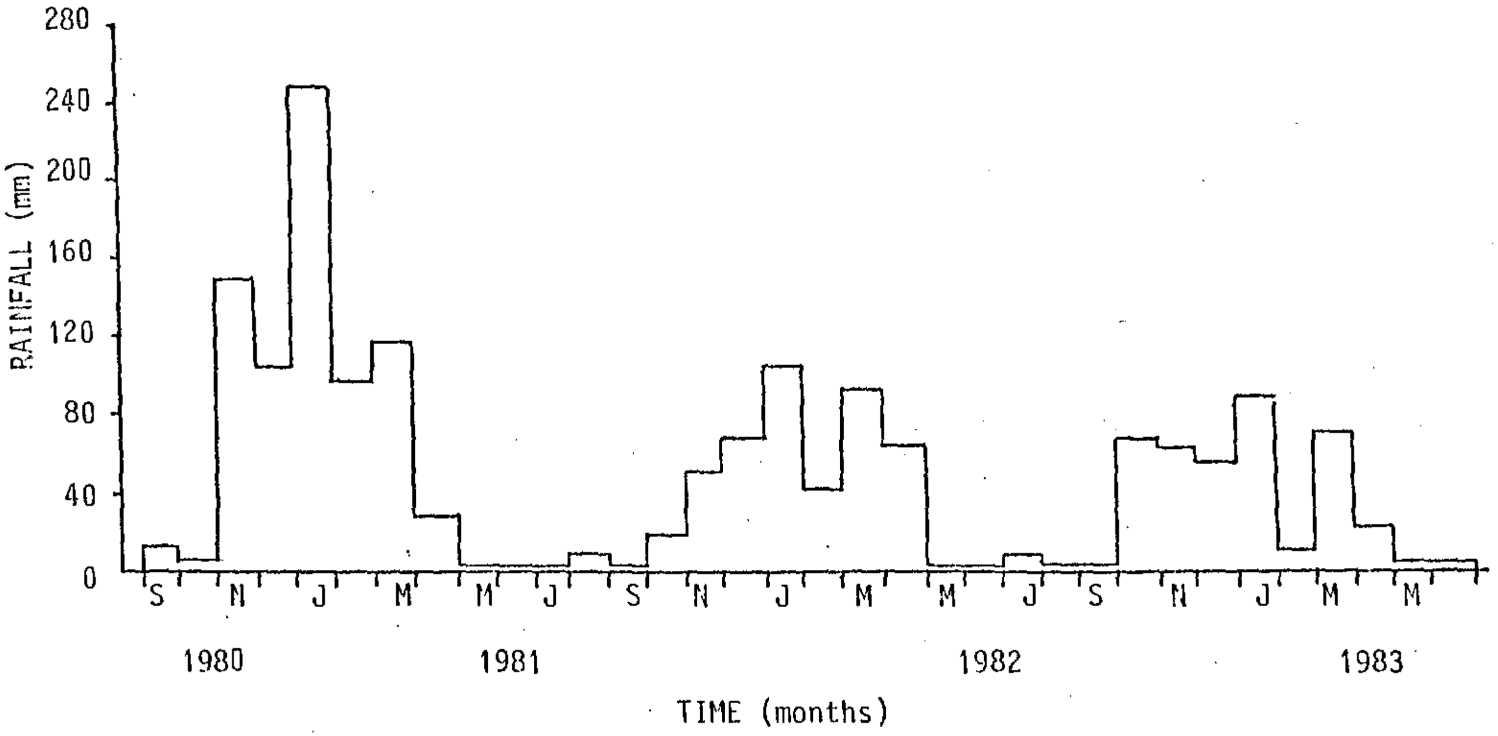
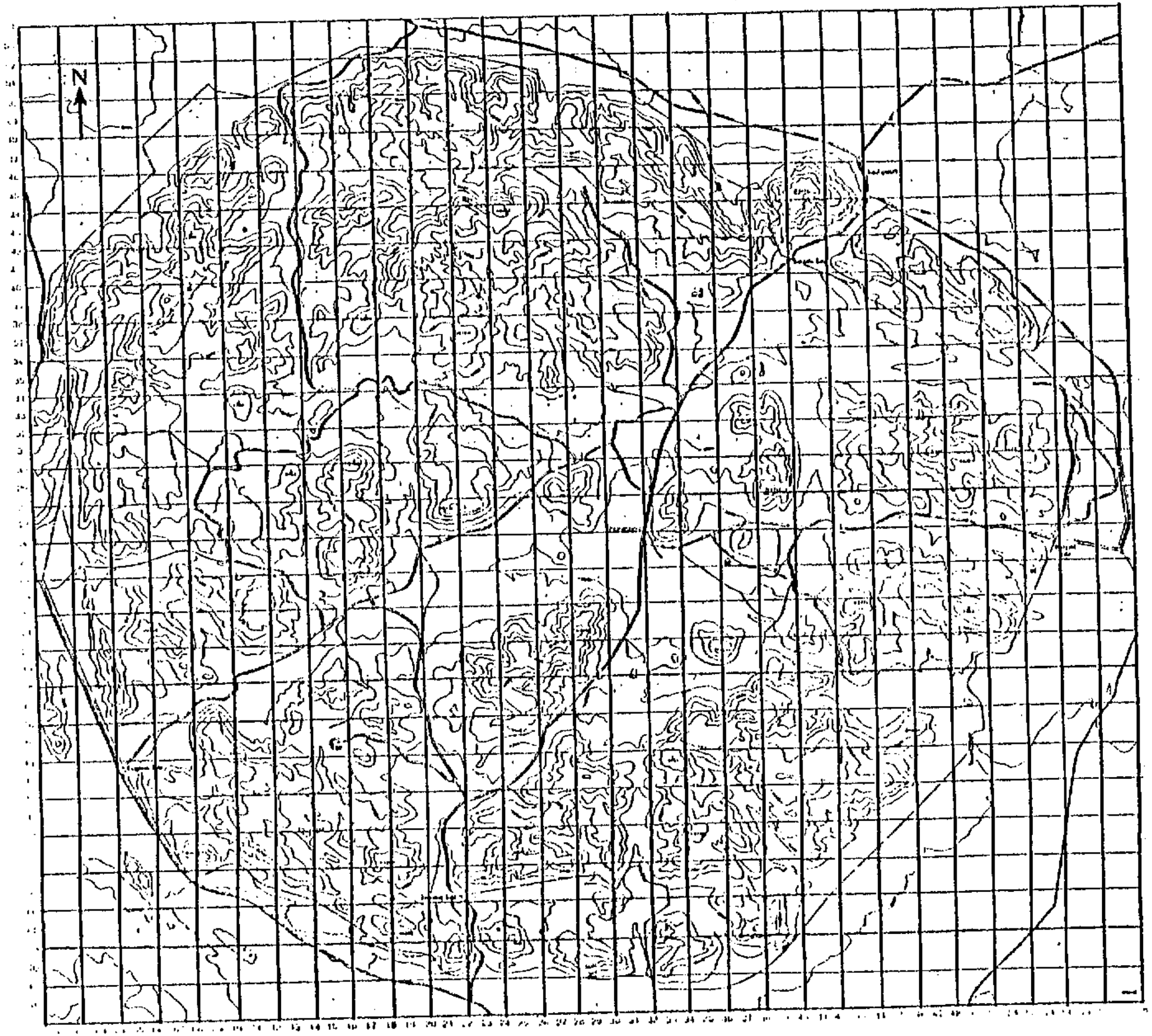


Figure 2.3 : Seasonal Differences in the Monthly Rainfall recorded at Manyane Gate in the Pilanesberg Game Reserve during the study period.

Figure 2.4 : Contour Map of the Pilanesberg Game Reserve.

<u>KEY</u>:

—·— = Boundary of reserve.
═══ = Roads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rocks forming the hill cores with their outcroppings indicated by dense tree cover. The syenites weather down to the sandier soils (dominated by tree species such as Combretum zeyheri), whereas the foyenites tend to weather down to the more clayier soils dominated by Spirostachys africana trees. The hill summits meet the well developed pediments, formed chiefly on latosols, and finally down to the valley floors. This formation thus depicts a catenal sequence.

2.4 Drainage

The reserve has a total of 21 catchment basins of which the Mankwe is the largest (178,7 sq. km). The radial drainage leaves the Pilanesberg ring complex by 16 poorts, all of which lead into the Crocodile branch of the Limpopo River (Tinley, 1978). Those streams radiating from NW, N and NE of the complex are caught by the Bierspruit tributary of the Crocodile River, and those from the SW, S, SE and E by the Elands River tributary. Most of these streams appear to be seasonal, except for the Mankwe and a number of its tributaries.

The largest perennial surface water is the Houwater Dam in the Mankwe valley (Figure 2.5). The numerous other small dams appear to be perennial only during the above average rainfall years. There are also a large number of boreholes scattered throughout the reserve which were constructed by white farmers, previously living in these areas.

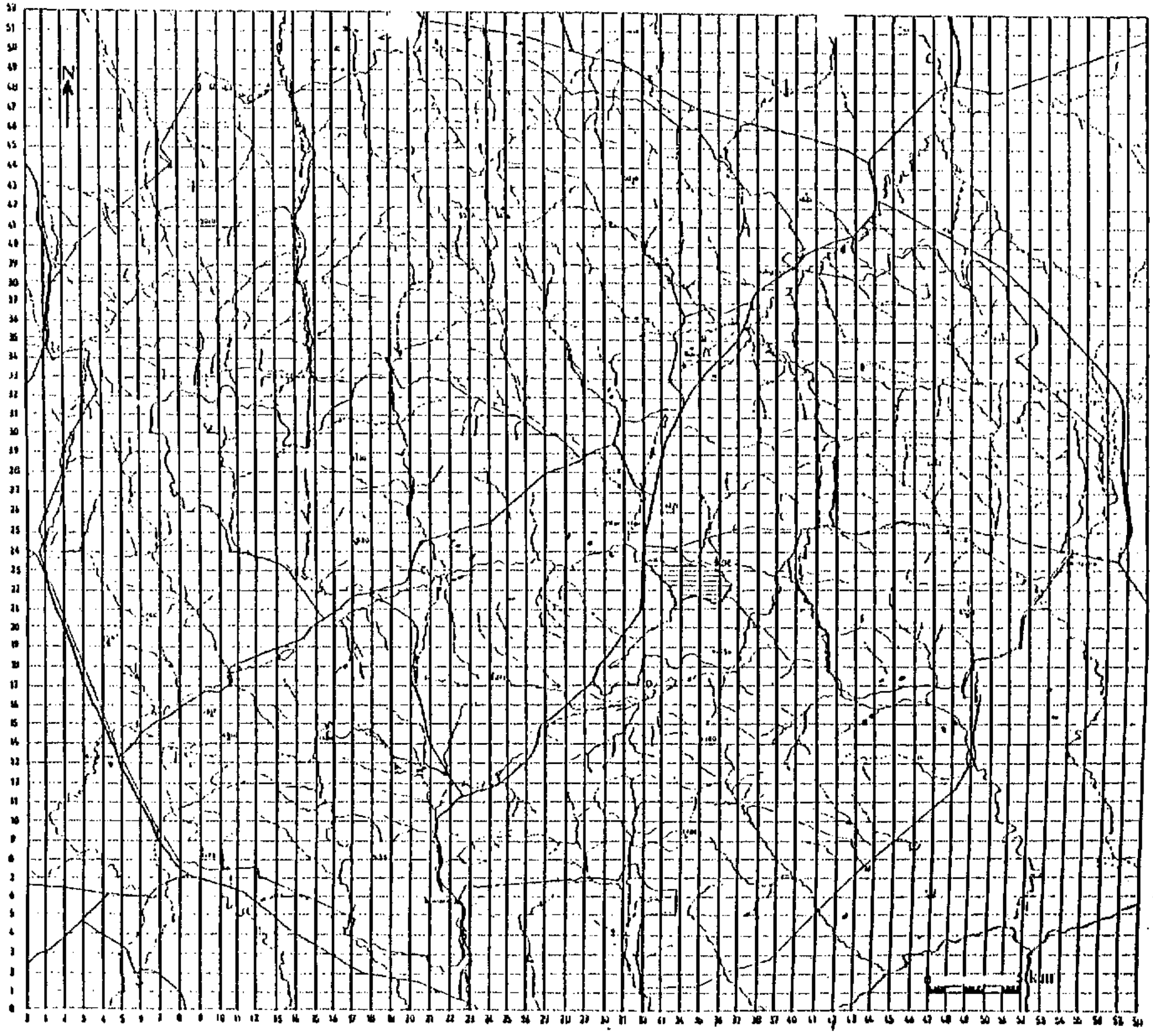
2.5 Vegetation

Adcocks (1975) describes the Pilanesberg vegetation as Sour Bushveld (Type 20). It is related to the vegetation found on the Waterberg, Magaliesberg and Soutspansberg mountain ranges which characterizes a typical duplex savanna system of tufty, wiry, sour grass species forming the ground cover, and short to medium trees forming the woody layer. The valley savannas, however, tend to be related more to Adcock's Turf Thornveld (Type 13) typical of the arid savanna communities characterized by Acacia mellifera

Figure 2.5 : A Map of Pilanesberg Showing the Perennial and Seasonal Streams and the Water Points.

KEY:

〜 = Perennial streams.
- - - = Seasonal streams.
▤ = Mankwe dam.
◇ = Water points.
◁ = Small dams.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mellifera tree species.

Tinley (1978) described the Pilanesberg system as having 5 major community types (refer to Figure 2.6);

(i) Aquatic communities, typical of running waters, e.g. streams, rapids and falls.

(ii) Grasslands, for example, summit grasslands occurring on the hill tops, sour pediment grasslands occurring on the seasonally high watertable soils with ferricrete (ouklip) sheets some 5 to 20cm below the surface, the valley floor grasslands occurring on the alluvial slope deposits, and secondary grasslands found on old fields.

(iii) Rockfaces or scree slopes formed largely by red syenites.

(iv) Savannas, for example, xerocline hill savannas, mesocline savannas, valley thorn savannas which form mosaics with thickets, and pediment savannas which are formed by bush encroachment on acid grasslands.

(v) Thickets, for example, the kloof thickets, riverine thickets, and the talus thickets found on the boulder scree slopes.

The reserve therefore depicts a habitat pattern typical of a catenary sequence with moist tree savannas on the hills, acid grasslands on the pediments, and a mosaic of arid and thorn thickets and scrub savanna in the valleys.

2.6 Fauna

According to Tinley (1978) most of the species occurring in southern Africa were found in this region. The most important large herbivores present in the reserve today are impala, mountain reedbuck, zebra, gemsbuck, kudu, tsessebe, sable, hartebeest, wildebeest, eland, giraffe, buffalo, white rhino, black rhino and elephant. The predator density is low relative to other reserves of similar size, the dominant species being brown hyena, cheetah (introduced) and leopard.

Figure 2.6 : Vegetation Map of the Pilanesberg Game Reserve.

KEY:

1 1 = Pediment grasslands.

∘ ∘ = Secondary grasslands.

● ● = Summit savannas.

× × = Mesocline savannas.

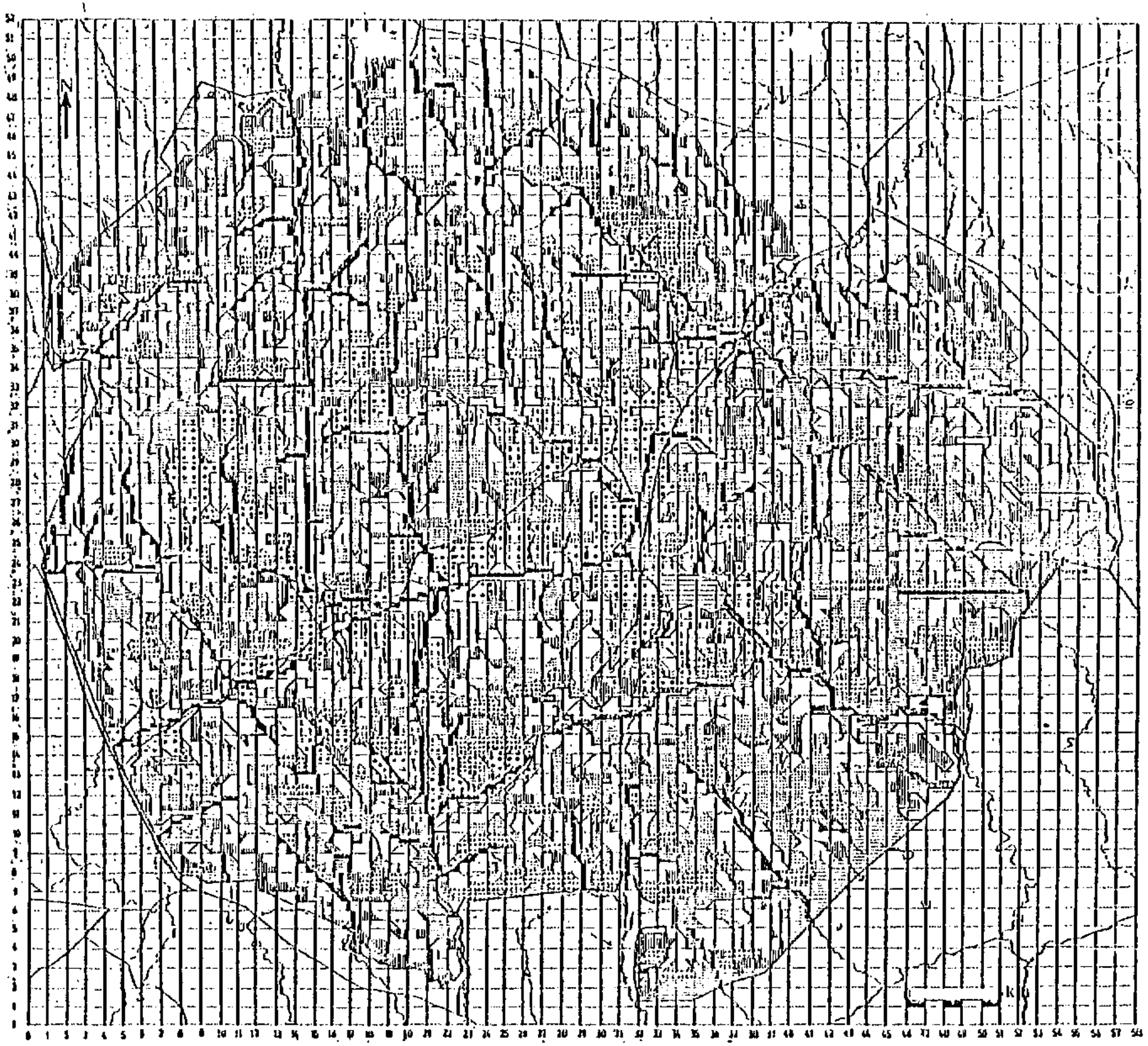
☐ = Xerocline savannas.

≡ = Valley savannas.

|||| = Talus thickets.

▣ = Valley thickets.

▩ = Riverine thickets.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2.7 Previous Land Use

Prior to the reserve's establishment in 1979, the area had been divided into a number of farms with cultivation being largely practiced in the more arable valleys. Simon Ratlau, a field worker for the Bophuthatswana Agricultural Department, confirmed that the "Pilanesberg landscape was practically bare or devoid of grass 10 years prior to its establishment". Since then these fields have developed into secondary grasslands of various successional stages. Thus, it is clear that the previous use of these lands, whether for cattle farming or cultivation activities, played an important role in structuring the present system. However, the degree to which the habitat has been altered, is unknown.

CHAPTER THREE

THE AVAILABLE RESOURCES

3.1 Introduction

Petrides, Golley and Brisbin (1968) pointed out that "populations of herbivores do not exist as separate entities, but are integral parts of the biotic environment". Thus, before attempting any study concerning the relationship between herbivores and their habitats, the types and quantity of resources available to the animals must first be identified. The basic requirements of ungulates can be broken down into four categories; food, water, protection from climatic extremes and protection from predators (Sinclair, 1977). In the Pilanesberg Game Reserve the first three needs are especially accentuated during the dry season when resources are least abundant and climate is most extreme. However predator avoidance by the grazers is negligible as predator densities are very low. The first two factors, namely food supply and water availability are considered to be the primary factors influencing herbivore distributions and habitat selections in the Pilanesberg Game Reserve. Thus the availability of these two factors has been analyzed in detail in this chapter. The next chapter deals with their importance in terms of herbivore habitat selection.

All herbivores, as primary consumers of plant material, are entirely dependent on food production and availability for their existence. This led Lack (1954) to postulate that food supply is the most important factor both limiting and regulating herbivore numbers. There are, however, a number of environmental factors, both natural and man-induced which influence the availability and production of forage to the herbivores, eg. rainfall. The availability of water has also been identified as a limiting factor in that it confines animal movements within the vicinity of water. For example, Western (1975) was able to show that although the ungulate populations in the Amboseli Nature Reserve generally select the best pastures available to them, in many cases accessibility was limited to certain regions restricted around the water supplies. Similarly, Blankenship and Field (1972) have shown that water availability is one of five major factors influencing the distribution of wild ungulates on a ranch in Kenya.

Thus, in all cases food availability was limited to those habitats within "cruising range" of permanent water (Western, 1975). It is for this reason that the importance of water to herbivore distributions must also be established before stocking densities in the Pilanesberg Game Reserve can be established.

This chapter first classifies the vegetation types in the reserve based on topography, woody vegetation density and herbaceous cover, thus providing the necessary habitat divisions to analyze herbivore habitat selection. These results can then be related to the seasonal changes in the herbivores' habitat selection. Finally, the importance of water to the grazers, is established.

3.2 Materials and Methods

3.2.1 Field Measurements and Data Collection

3.2.1.1 Vegetation Types

One hundred and sixty transects were sampled in apparently homogeneous patches of vegetation so as to cover the vegetation variability in the reserve. The transect positions were determined both from aerial photographs and a reconnaissance of the area. The information used in the classification was based on the data collected mainly from a monitoring programme supervised by Walker (1982) and initiated in December 1980. Approximately 100 transects were measured during this programme. In each transect information was collected on both the woody and the herbaceous vegetation. However, classification of the habitats was based only on the herbaceous vegetation as all the herbivores under consideration were largely grazers. The location of the vegetation transects are shown in Figure 3.1.

Fifty, one-metre square quadrats were positioned at approximately 5 m intervals along a 50 m transect line. In each quadrat the herbaceous species composition was determined by bulk contribution using the method developed by Mannetjie and Haydock (1963). In each quadrat an estimate is made of the species which contributes most to the biomass and is assigned a rank of '1'. Similarly the species that contributed second and third in the overall biomass were assigned ranks of '2' and '3' respectively. In order to estimate the total percentage contribution of the species in that vegetation type, constants were determined by Mannetjie and Haydock (1963). These constants which can be interpreted as the contribution of the rankings to the biomass, are 70,2%, 21.1% and 8.7% for rankings 1, 2 and 3 respectively. The proportion of quadrats in which the species was 1, 2 or 3 were then multiplied by their constants to yield the percentage bulk contribution of each species to the herbaceous vegetation.

3.2.1.2 Water Availability and Herbivore Distributions

The distributions of the permanent and ephemeral water supplies were located by aerial surveys conducted by staff members of the reserve. The water points were then plotted on a map with a 500 x 500m grid system. Two surveys were conducted, one during each season (ie; wet and dry seasons).

Observations of herds and single animals were made while driving along the road transects shown in Figure 3.1. The sightings were recorded and their locations plotted on a map with a 500m x 500m grid system. In addition, information on the herd or group size, sex, age, and identification number, if present, was also noted.

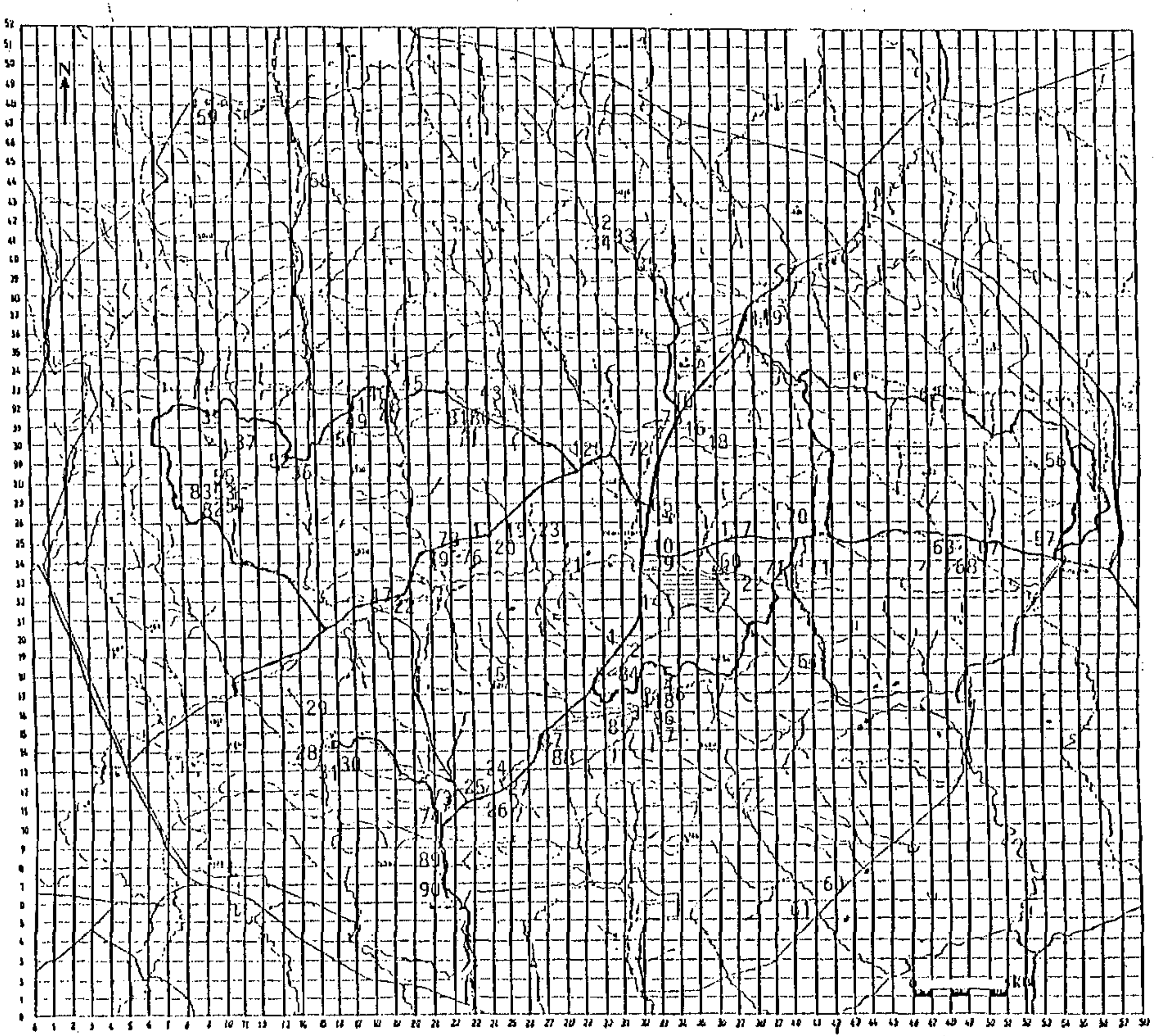
This information was then typed into an Apple II microcomputer using a data base programme developed by Erica Harris (see Dickinson, 1983). The main reason for using this system was that large amounts of data could be stored, analyzed and retrieved at any time. A programme was also developed using the Apple

Figure 3.1 : Locations of the Vegetation and Road Transects.

KEY:

16 = Vegetation transect sites.

⌒ = Road transects.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Graphics package, to display the data on a map of the Pilanesberg Game Reserve (Dickinson, 1983). Thus, a better picture of both the seasonal distributions of the species and the water points could be displayed on a map and analysed.

3.2.2 Data Analysis

3.2.2.1 **Vegetation Classification**

The aim of classification studies is to group similar entities together in clusters based on the abundance of species in a number of samples or transects.

A classification was done on the herbaceous vegetation using a hierarchical multivariate technique known as Two-way Indicator Species Analysis (TWINSPAN). TWINSPAN is analogous to the Braun Blanquet method of phytosociology (Moore, 1962) and was preferred because, with the quantitative data available, a more sophisticated analysis was neccessary.

3.2.2.1.1 Two-way Indicator Species Analysis

The computer program, TWINSPAN, was developed by Hill(1979) for the Cornell Ecological Program series. It is a "polythetic divisive" technique in which the data are first ordinated by reciprocal averaging, (Hill, 1973) and then divided or grouped, (Gauch and Whittaker, 1981) in a hierarchical manner.

Reciprocal averaging is generally used to reveal correspondences between observations on two kinds of information, e.g. samples and species. It was first developed by Hirschfield (1935) and Fisher (1940) and has been termed "Correspondence Analysis" (Benzecri, 1969; Escofier-Cordier, 1969). It is essentially an ordination technique related conceptually to weighted averages, but computationally to Principal Component Analysis (Gauch, 1982). The species are first weighted by positions along an initial gradient and are then used to calculate sample-scores. These weighted sample-scores are then used to calculate a new and improved calibration of the species. The new weighted score now provides a further improvement in the sample calibration. Back-and-forth, iterative calculations lead to a stable, optimal solution which does not depend on the initial arrangements (Gauch, 1982). This process has been termed Reciprocal Averaging because the species-scores are averages of the stand scores and reciprocally, the stand- scores averages of the species-scores.

When insignificant changes result from one iteration to the next the solution stabilizes and the scores range from 0-100. The contraction in the range of the species-score in one iteration (after convergence is reached), is the eigen value. A second axis may then be taken out using the same method by correcting for the first axis, a third axis may then be calculated while correcting for the first two, and so on. Higher axes may be scaled onto the range proportional to the square root of their eigen values.

Like Principal Component Analysis, Reciprocal Averaging can be used geometrically as a derivation of new axes; which maximally account for the structure of the points in a multidimensional cloud of points, making possible the reduction of the dimensionality (Gauch, 1982).

Gauch (1982) recommended Two-way Indicator Species Analysis (TWINSPAN) for hierarchical classification for the following reasons;

1. its effectiveness,
2. its robustness,
3. its use of the original vegetation data rather than secondary similarity matrices,
4. it integrates the classification of both samples and species,
5. it orders the sample sequence in a dendogram so that the most similar samples are placed together, and
6. it is economical in terms of computer requirements.

The algorithm of TWINSPAN produces a two-way table, similar to a

Braun-Blanquet table, and identifies several species which are diagnostic of each division. Two-way Indicator Species Analysis makes repeated dichotomies of both the sample and species by dividing the axis in half (Hill, 1979). The differential species at the extremes of the ordination axis are first identified. Then the samples are divided into two clusters near the middle of the axis. The sample division is then refined by reclassification using the differential species. The process is repeated on the two subsets to give four clusters, and so on until each cluster has no more than a chosen minimum number of members (Gauch & Whittaker, 1981). The grass species are classified in the same way except the classification is now made using samples. The classification is made on the basis of fidelity, which is the degree to which species are confined to particular groups of samples.

3.2.2.2 Test for Randomdess in Herbivore Distributions

The assumption being that is if the herbivores are distributed randomly within the reserve then their distributions will be proportional to different areas around the water points. In other words the percentage number of total observations should increase as the area from the water points increases. The expected values were calculated using above results and then tested against the actual values using a Chi-square test.

3.3 Results and Discussion

3.3.1 Classification of the Herbaceous Vegetation

The aim of this section is firstly to classify the habitat types based only on the herbaceous vegetation, and secondly, to compare this classification to that of Tinley's (1978).

The herbaceous vegetation data matrix consists of 35 grass species and 160 transects.

3.3.1.1 Two-way Indicator Species Analysis (TWINSPAN)

The divisions based on TWINSPAN are shown in dendrogram form in Figure 3.2.

This technique depicted no clear-cut distinctions except for those sites which had been recently disturbed either by heavy grazing or by agricultural activities (eg. Secondary grasslands and Cynodon dactylon "lawns") and those showing little signs of disturbance (eg. Pediment grasslands and some savannas). The results are discussed in more detail below.

The grasslands studied were found to be characterised by the following indicator species; Cynodon dactylon (CYDA), Rhynchyletrum repens (RHRE), Heteropogon contortus (HECO), Themeda triandra (THTR), Hyparrhenia hirta (HYHI), Elyonurus argenteus (ELAR), or Bothriochloa insculpta (BOIN). Other prominent grasses were Urochloa mosambicensis(URMO), Eragrostis rigidior (ERRI), Aristida congesta (ARCO), Panicum deustum (PADE), Loudetia flavida (LOFL) and Cymbopogon species (CYMB).

Level 1: (n = 160). In the first division, a distinction was made between different successional stages i.e. from generally climax grasslands and savannas on the one hand, and secondary or oldland grasslands and heavily utilised Acacia thickets on the other. The indicator species for this division were Themeda trianda (THTR), Heteropogon contortus, (HECO) and Elyonurus argenteus (ELAR) for the former, and Cynodon dactylon (CYDA) for the latter.

Level 2 1. (n =84). The later successional or climax stages (including savannas and woodlands) are further separated into those dominated by Heteropogon contortus (HECO) and those dominated by Themeda triandra (THTR) and Elyonurus argenteus (ELAR) and Hyparrhenia hirta (HYHI). The indicator species being Panicum coloratum (PACO), Themeda triandra (THTR) and Elyonurus argenteus (ELAR). The first group is characteristic of the more open grasslands including the pediment grasslands. The second group appears to characterize those sites which are generally

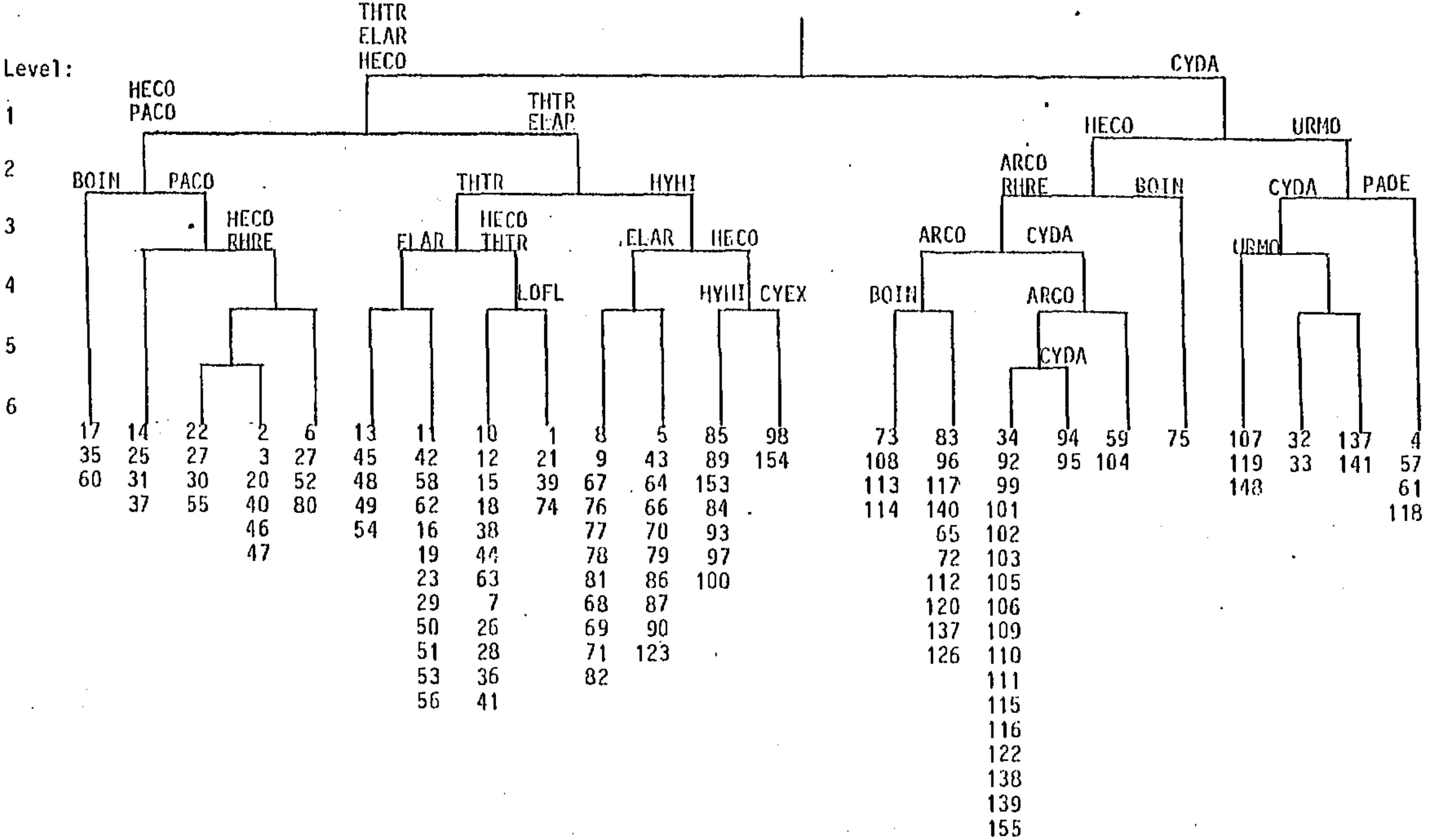


Figure 3.2 : Classification of the Herbaceous Vegetation using TWINSPAN (Hill, 1979). A key to the Indicator Species used to characterize the different grasslands are given in Appendix F.

more wooded with higher canopy covers (eg. savannas).

2. (n = 76) The second group, namely the secondary grasslands and thickets, was divided into sites dominated by either Heteropogon contortus (HECO) or Urochloa mosambicensis (URMO). These indicator species separate the secondary grasslands and savannas from the more heavily utilized thickets.

Level 3 1. The next division separates sites which are dominated by either Bothriochloa insculta (BOIN) and Panicum coloratum (PACO) as their dominant species. Further divisions were unnecessary because they were difficult to interpret as the sites were separated on the individual dominant species alone.

2. This division appears to separate the valley savannas into sites dominated by either Themeda trianda (THTR) or Hyparrhenia hirta (HYHI). It is interesting to note that both groups are further divided into sites dominated either by Elyonuris argenteus (ELAR) or Heteropogon contortus (HECO).

3. This division uses Aristida congesta (ARCO) and Rhynchelytrum repens (RHRE) to separate the secondary grasslands from the sites dominated by Bothriochloa insculpta (BOIN). The secondary grasslands can be further divided into sites dominated either by Aristida congesta (ARCO) or Cynodon dactylon (CYDA) (eg. termitaria).

4. Two grassland types are distinguished in this division, namely, those dominated by Cynodon dactylon (CYDA) and Urochloa mosambicensis (URMO) and those dominated by Panicum deustum (PADE). No further levels will be discussed because of the difficulty in identifying indicator species which suitably distinguish one type from another.

The results obtained from this technique were then compared to Tinley's (1978) classification which was based largely on topography and woody vegetation. He recognised six major vegetation types (refer to chapter two);

(i) Secondary grasslands or oldlands,
(ii) Pediment grasslands,
(iii) Valley savannas,
(iv) Mesocline savannas,
(v) Xerocline savannas, and
(vi) *Acacia* and riverine thickets.

Both the summit grasslands and talus thickets have been omitted because of limited importance in terms of white rhino habitat selection. These vegetation types were then compared to those distinguished on the basis of grass species alone using the TWINSPAN analysis. Five basic habitat types were recognized using the TWINSPAN programme;

(i) *Cynodon dactylon* "lawns" (level 3, sublevel 4),
(ii) Secondary grasslands, characterized by *Aristida congesta* and *Rhynchyletrum repens* (level 3, sublevel 3),
(iii) Pediment grasslands (level 2, sublevel 1),
(iv) Wooded savannas (level 3, sublevel 2), and
(v) Thickets, dominated by *Panicum deustum*, *Cynodon dactylon* and *Urochloa mosambicensis* (level 3, sublevel 4).

Although no clear-cut distinctions were apparent, habitats could be classified on a similar basis to that of Tinley's (1978) except for the more subtle features, eg. the savannas dominated either by *Themeda triandra* or *Hyparrhenia hirta*. The *Cynodon dactylon* "lawns", although occupying only approximately 2% of the reserve, were included because of their high selection by most herbivores. No clear cut distinctions were made between the valley and hillside savannas, but this may have been due to a low sample size. However, the savannas were divided into either valley or hillside based on topography alone. It should finally be noted that even within these fairly distinct habitats, patchiness or heterogeneity was apparent.

Table 3.1 summarises the vegetation types in terms of the percentage species composition and the proportion of the low,

Table 3.1 : The Herbaceous Species Composition of each vegetation type with the palatability (PALAT.) of each species (P = palatable, I = intermediate and U = unpalatable; PAL., INT. and INT. are the proportions of palatable, intermediate and unpalatable grass species, respectively).

	VEGETATION TYPES						
SPECIES	Secondary Grassland	Pediment Grassland	Valley Savanna	Hillside Savanna	Thicket	Termitaria and *Cynodon* patches	PALAT.
Cynodon dactylon	12.4	1.5	6.2	0.0	13.2	11.2	I
Aristida congesta	3.2	11.2	2.5	3.3	0.6	3.7	I
Rhynchelytrum repens	9.4	4.0	3.4	1.3	0.2	2.8	I
Heteropogon contortus	14.8	14.4	15.7	39.5	5.5	8.7	P
Themeda triandra	3.7	1.0	4.9	8.4	7.2	0.6	P
Eragrostis curvula	4.1	1.1	2.4	0.0	4.4	7.3	I
E. superba	9.4	1.3	2.4	0.0	3.2	8.5	P
E. rigidior	5.9	1.6	2.1	0.0	1.9	9.3	I
E. chloromelis	0.0	2.8	3.1	0.0	0.1	0.0	I
E. racemosa	0.2	1.7	0.5	0.0	0.7	0.0	I
E. plana	0.1	0.0	0.1	0.0	0.0	0.0	I
E. gummiflua	0.7	4.1	0.4	0.0	1.8	0.0	I
Elyonuris argenteus	3.1	26.4	27.6	5.3	6.6	0.4	U
Cymbopogon excavatus	2.3	9.2	6.0	0.9	2.3	1.9	U
Hyparrhenia hirta	8.0	17.7	4.9	0.0	1.5	1.5	I
Trichoneura grandeglumis	0.6	1.7	0.3	0.0	0.0	0.4	I
Bothriochloa insculpta	0.0	0.0	0.8	0.0	3.2	1.9	I
Brachiaria serrata	1.1	1.4	0.9	10.2	0.5	0.2	P
Urochloa mosambicensis	4.9	0.0	1.7	0.0	10.6	17.6	P
Setaria flabellata	0.2	0.2	0.7	0.0	1.3	0.0	I
Loudetia flavida	0.0	3.7	1.1	10.9	0.1	0.0	I
Digitaria eriantha	2.5	2.2	1.6	0.0	7.1	0.7	P
Microchloa caffra	0.0	0.0	0.7	0.2	0.1	0.1	I
Tragus berteronianus	0.4	0.0	0.7	0.0	0.9	0.3	I
Panicum deustum	0.0	1.4	0.9	0.0	7.3	0.7	P
P. coloratum	0.0	1.0	2.5	0.0	8.6	2.9	P
Pogonarthria squarrosa	0.3	0.6	0.1	0.0	0.0	0.1	I
Sporobolus species	1.7	3.0	0.4	16.2	2.2	1.0	I
Chloris virgata	0.0	0.0	0.3	0.0	4.2	5.4	I
Setaria nigrirostris	0.2	0.0	0.8	0.0	1.7	0.0	I
Perotus patens	0.0	0.0	0.1	0.0	0.3	0.1	I
Eragrostis species	4.0	3.0	1.3	0.0	2.2	4.0	I
PAL.	43.9	21.7	34.7	58.1	52.2	51.0	
INT.	50.7	42.7	31.7	35.7	38.9	46.7	
UNP.	5.4	35.6	33.6	6.2	8.9	2.3	
AREA (ha)	3119	1628	7322	23366	7534	± 20	

medium and high palatable grass species. The degree of palatability was based on the herbivore preferences. Grass species, for example, Heteropogon contortus and Urochloa mosambicensis were regarded as palatable whereas, species such as Bothriochloa insculpta, Elyonuris argenteus and Cymbopogon excavatus as unpalatable.

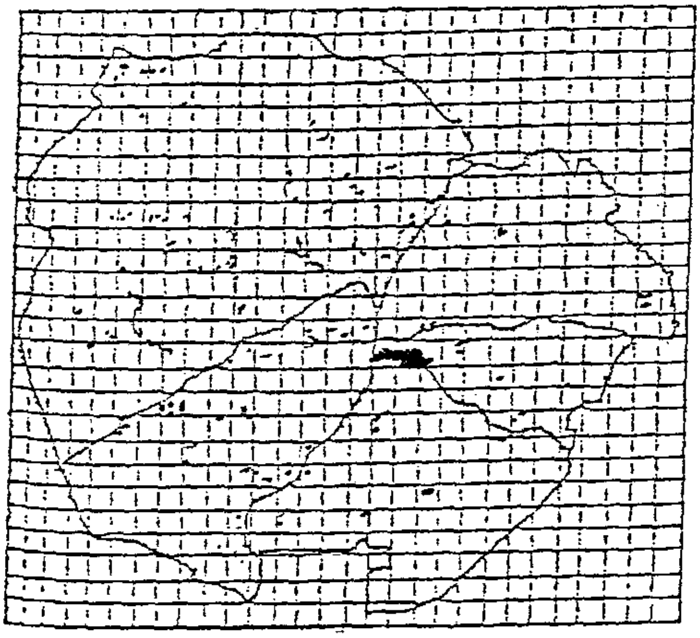
3.3.2 Relationship between Water Availabilty and Herbivore Distributions

A map of the wet and dry season water distributions is given in Figure 3.3. It is evident that the water availability in the reserve can change markedly from one season to the next with the maximum distance of any point in the reserve to the nearest water point increasing as rainfall decreases. This seasonality in water availability should greatly influence the herbivore movement and their distributions, as predicted by Western (1975).

The distribution of distances of the herbivores to the nearest available water supplies are given in Figures 3.4 to 3.8. All species showed a high concentration around the water points indicating that water does tend to restrict the herbivores movements within limited distances. The mean distance at which the herbivores were sighted from the nearest water supply varied from 659 m (zebra) to 946 m (impala) during the wetter months, and 1012 m (hartebeest) to 1319 m (impala) during the drier months. Significant differences ($P < 0.001$, using the Chi-square test) between the herbivores and the nearest water were apparent between seasons. Although water certainly appears to influence animal distribution patterns, movement away from the water supplies is evident during the drier months. This may indicate that the distribution limits from the water supply of the herbivores increases when water becomes limiting.

However Western (1975) estimated the distribution limits of the water dependent species (eg. impala) to be between 10 and 15km. The maximum distance from any point in the Pilanesberg Game Reserve to a water source during the dry season was approximately

(a) Wet Season



(b) Dry Season

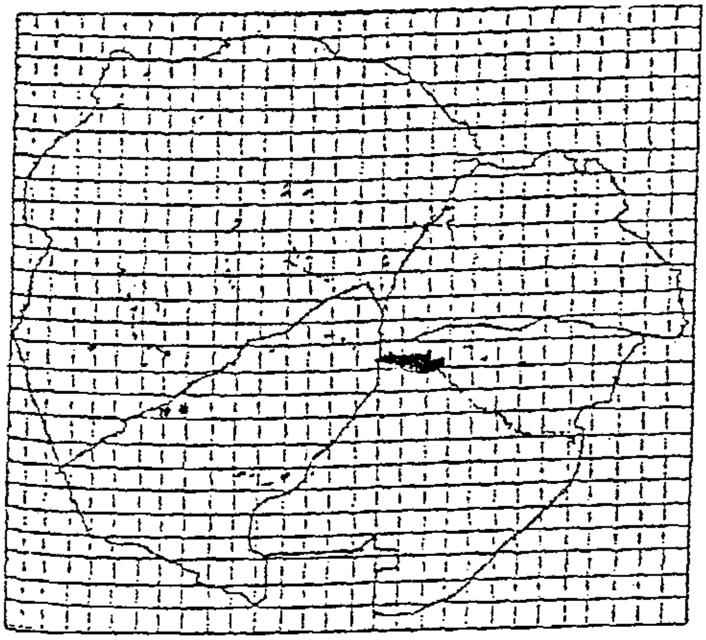
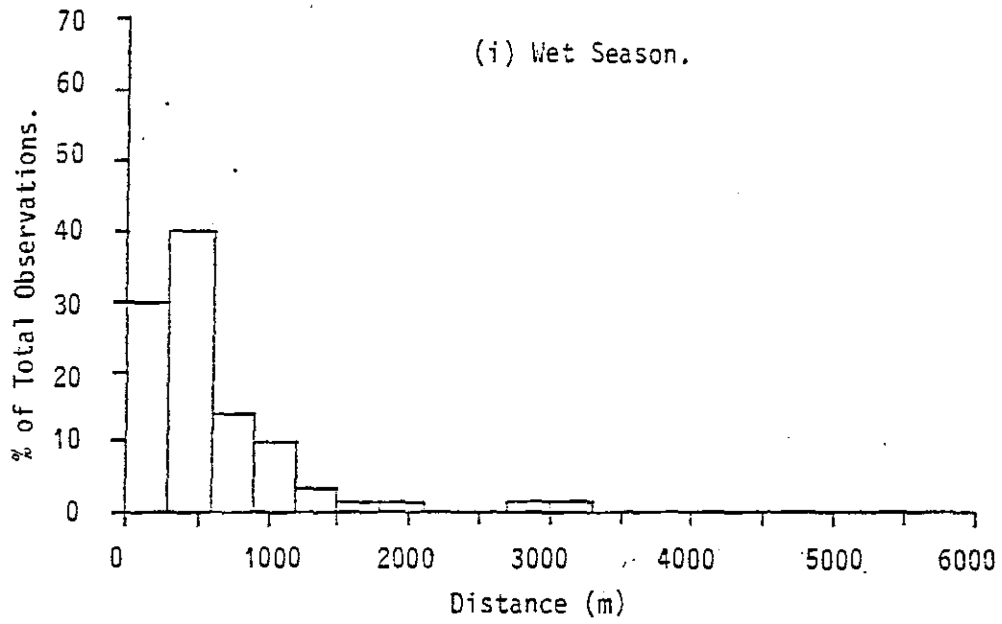


Figure 3. 3 : The Seasonal Distribution of Water Points in the Pilanesberg Game Reserve.



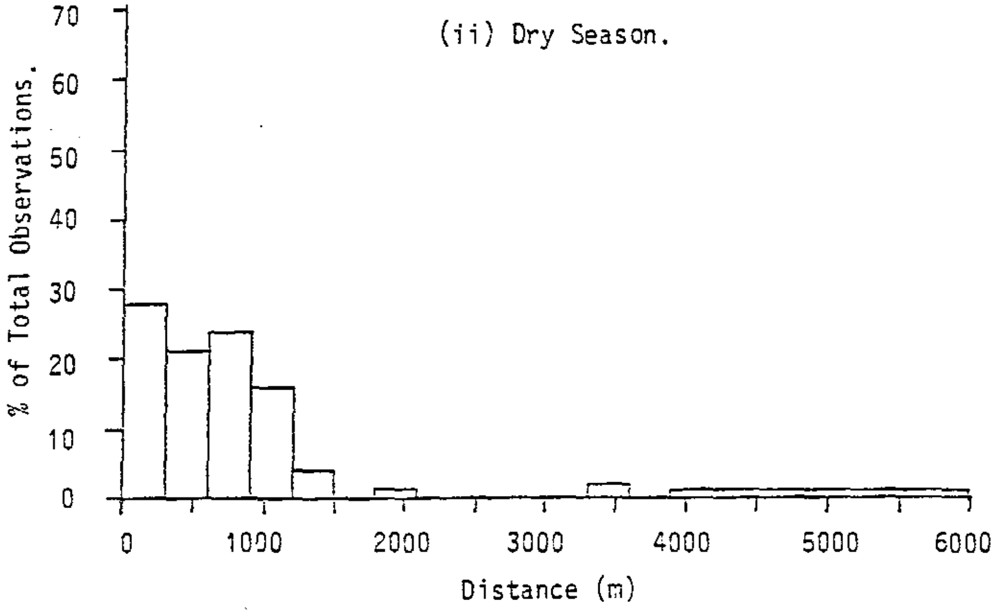


Figure 3.4 : The relationship between the percentage occurence of white rhino sightings and distance to nearest water.

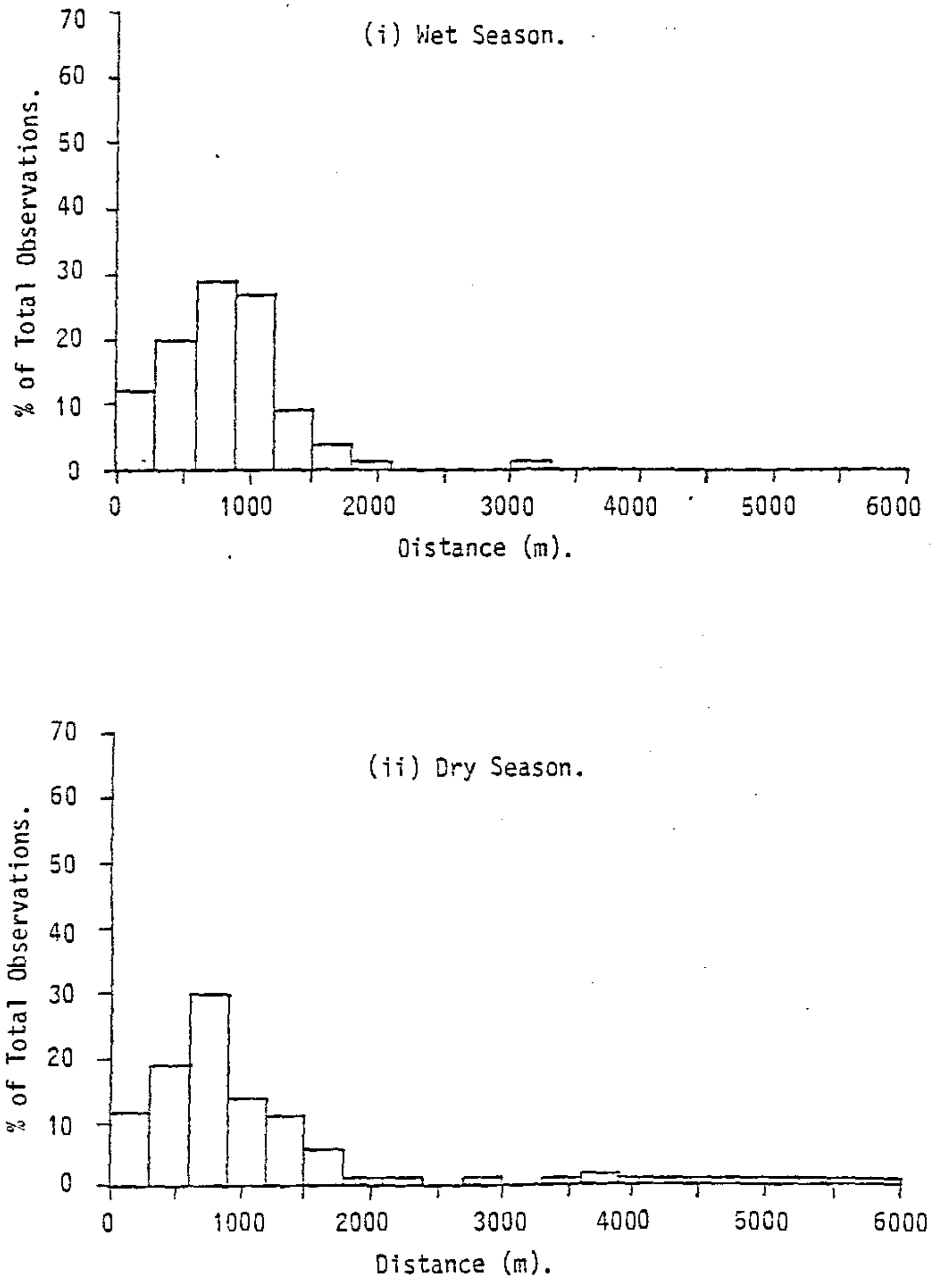
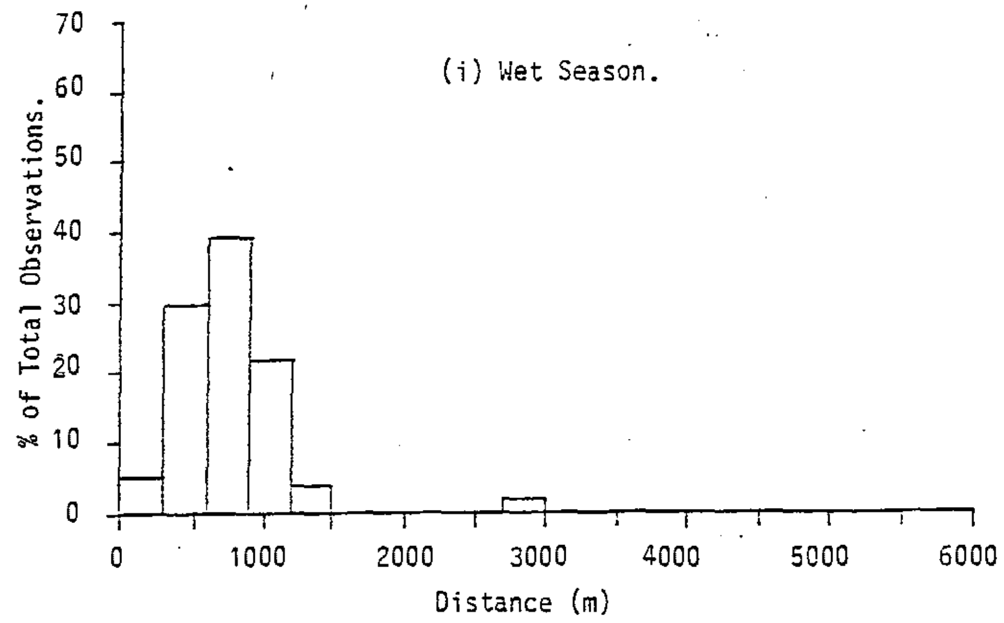


Figure 3. 5 : The relationship between percentage occurrence of hartebeest sightings and distance to nearest water.



(ii) Dry Season.

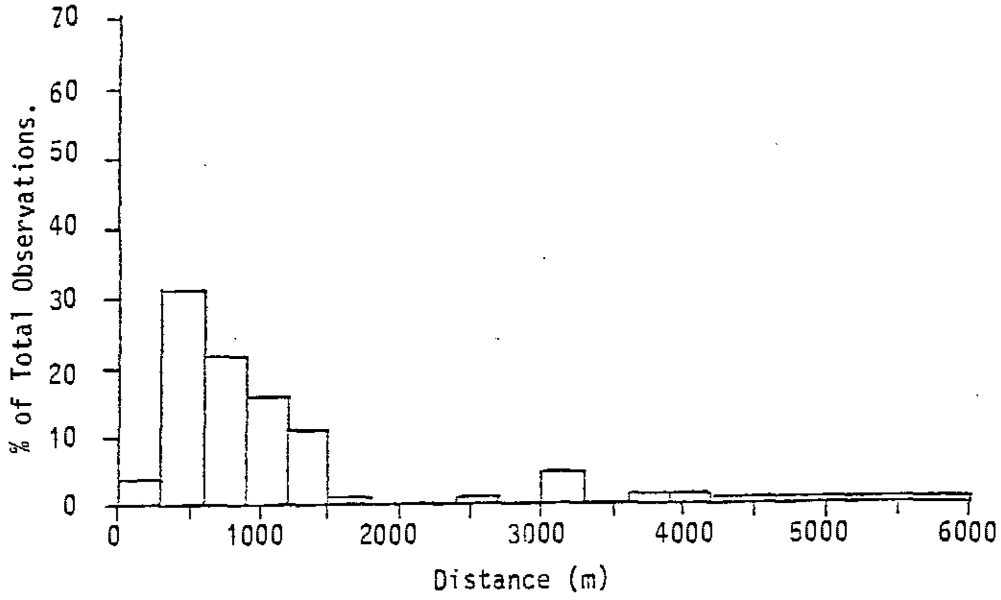


Figure 3.6 : The relationship between the percentage occurrence of wildebeest sightings and distance to nearest water.

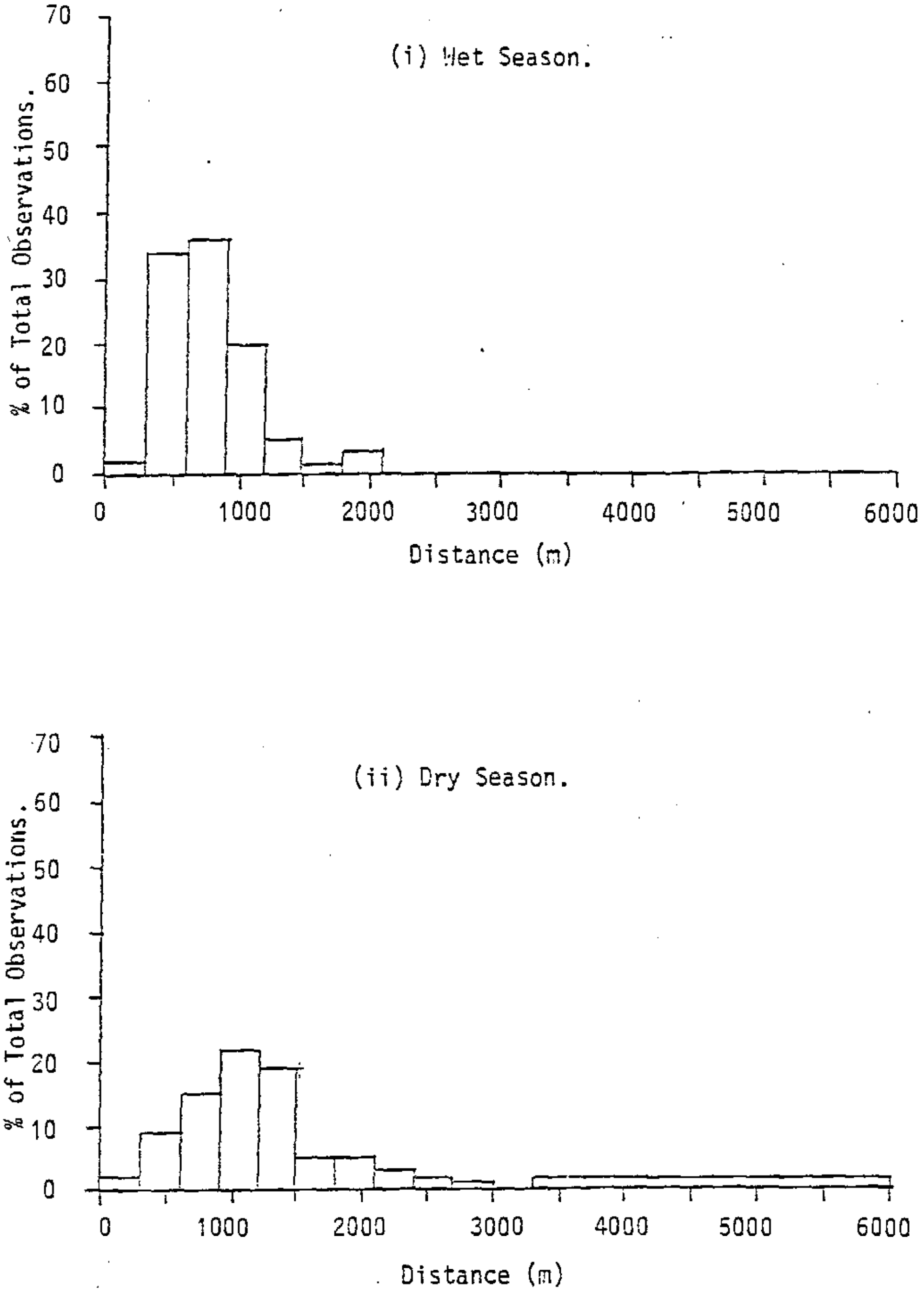
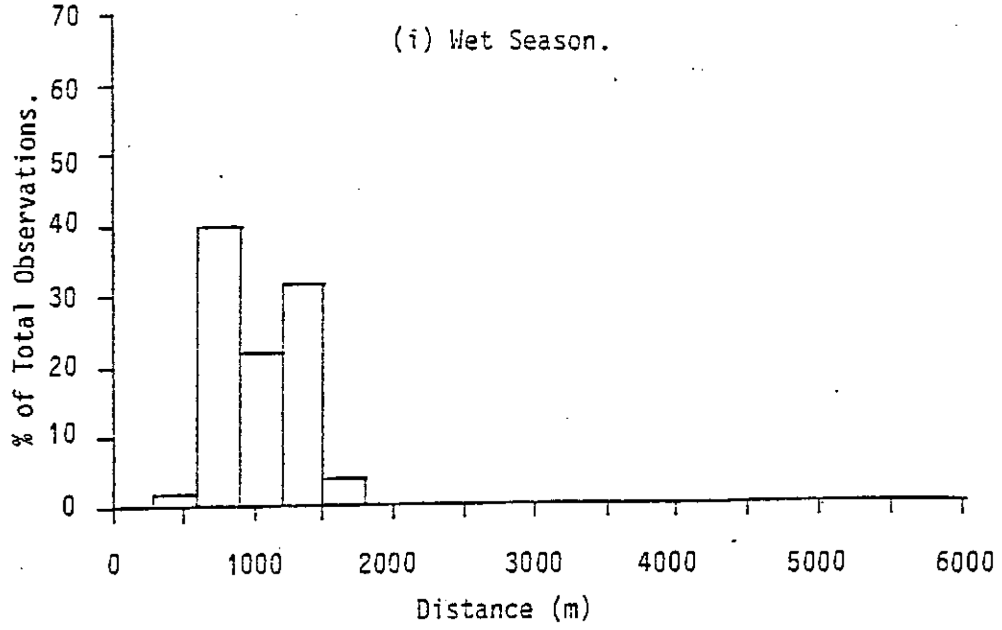


Figure 3. 7 : The relationship between the percentage occurrence of zebra sightings and distance to nearest water.



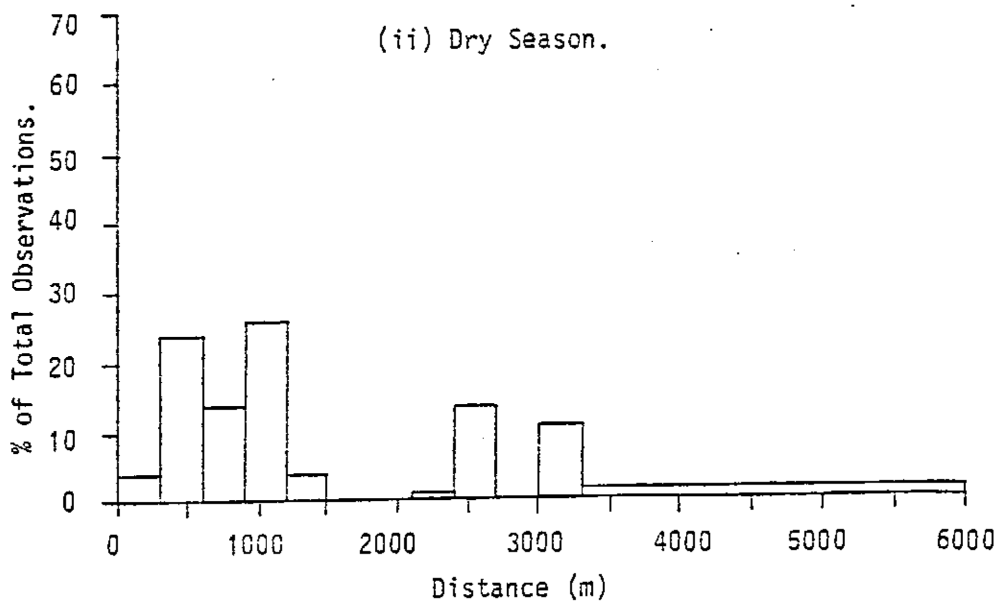


Figure 3.8 : The relationship between the percentage occurence of impala sightings distance to nearest water.

10km as opposed to 30km in the Amboseli Nature Reserve (Western, 1975). Hence, all the habitats in the reserve are within walking distance from the water points. Therefore, any herbivore less than 15km from a water source should not be limited by water. However, there may be other behavioural and social factors which may influence their distribution patterns. Hence, although water availabilty is an important requirement of the herbivores in Pilanesberg, its importance in affecting their present distributions is slight.

Water may also affect herbivore movement and distribution indirectly through the vegetation. Habitats are generally more productive the closer they are to water, and thus consequently lead to preferential selection by the grazers. It should however be noted that most of the available habitats chosen by the herbivores in the Pilanesberg Game Reserve are located in the valleys, which collect much of the water from the watersheds.

3.3.3 Biomass of the Herbaceous Vegetation

The mean values for the overall above ground herbaceous biomass for each habitat type are given in Table 3.3. Significant seasonal differences were found for each habitat. A significant decrease in the herbaceous standing crop occurred for both the secondary grasslands and the thickets (Appendix L) whereas the pediment grasslands and valley savannas increased from the end of the wet season to the end of the dry season. These differences can be accounted for by two reasons. Firstly, the increase in standing crop was probably due to an uncontroleable burn which swept through 60% of the reserve during August of 1980 resulting in a high production. The decrease in the standing crop for the other two habitats may have resulted from their relatively higher herbivore densities. Consequently, offtake by the herbivores was much higher in these habitats (see chapter 4).

Using the vegetation transect data, approximate biomasses for the three forage types (defined earlier) could be estimated within each habitat (Table 3.4). These results indicate that of the four

Table 3.3 : Seasonal variation in the above ground herb biomass (kg/Ha) each vegetation type. Standard errors are given in parentheses.

Season	Secondary Grassland	Pediment Grassland	Valley Savanna	Thickets
Late-wet	3000(168)	3200(920)	2840(1200)	1200(720)
Late-dry	2250(900)	4010(184)	3330(1220)	550(600)

Table 3.4 : Seasonal variation in the biomass (kg/Ha) of the three forage types for each habitat.

SEASON	FORAGE TYPE	HABITAT			
		SECONDARY GRASSLAND	PEDIMENT GRASSLAND	VALLEY SAVANNA	THICKETS
LATE-WET	PALATABLE	1320	704	994	624
	INTERMEDIATE	1530	1376	908.8	468
	UNPALATABLE	150	1120	937.2	108
LATE-DRY	PALATABLE	990	8B2.2	1165.5	286
	INTERMEDIATE	1147.5	1724.3	1065.6	214.5
	UNPALATABLE	112.5	1403.5	1098.9	49.5

habitats measured, the secondary grasslands account for most of the palatable biomass at the end of the wet season. However, at the end of the dry season, the valley savannas accounted for a high proportion of these species. The thickets, although supporting the highest proportion of palatable species, contribute the least to the overall palatable standing crop.

These results can now be related to seasonal changes in herbivore habitat selection (next chapter). In addition, the overall plant biomass for each habitat can be compared to those predicted from the model described in chapter seven. These results will therefore provide a means of testing the validity of the model.

CHAPTER FOUR

HABITAT AND FOOD SELECTION BY THE GRAZING UNGULATES AT PILANESBERG

4.1 Introduction

This section investigates the relationship between the large grazers (especially the white rhinoceros) and their habitat use, in terms of habitat and food selection.

Ungulates often show characteristic patterns of seasonal movement from one part of their range to another. Duncan (1975) identified two types of movements. The first is when the population moves as a coordinated unit, so that the annual ranges of the individuals are of the same order of magnitude as the range of the population (e.g. the Serengeti wildebeest, Watson, 1967), The second, occurs when the individuals show clear seasonal movements which are small compared to the population range. This type of movement is characteristic within most game reserves which support large ungulates. However the first type is seldom observed in reserves because movement is mostly prevented by the fenced boundaries.

In both cases the effect is to place the animals in a different environment. Thus there is a close relationship between habitat and movement. The response of an individual to vegetation structure that differs from the "optimum" is to move away from it. For example, Sinclair (1974) suggested that the buffaloes in the Serengeti select particular habitats in the dry season because it is in these that the optimal food is found. Pienaar (1974) in classifying the environmental factors (physical, historical and biotic) governing the distribution of herbivores stated that the vegetation was the all important. A number of ecologists (e.g. Petrides, 1956; Darling, 1960; Grzimek and Grzimek, 1960; Lamprey, 1963; Vesey Fitzgerald, 1965; Anderson and Talbot, 1965; Simpson and Cowie, 1967; De Vos, 1969; Field and Laws, 1970; Ferrar and Walker, 1974; Pienaar, 1974 and Hirst, 1975) have shown that ungulates exhibit a heterogeneous distribution over African vegetation types. This they attributed to be directly related to the varying degrees of habitat selectivity in a heterogeneous environment.

There are many qualitative reasons as to why animals select particular habitats, including the need to avoid predators, requirements of shade, food and water. Talbot and Talbot, 1963; Watson, 1966; Pennycuick, 1975; and Inglis, 1976 on the other hand have shown rainfall to be the proximate factor influencing wildebeest movement and habitat selection.

It is therefore necessary to isolate those environmental factors to which the animals respond when selecting for particular habitats. Western (1973) was able to show that the grazing ungulates in the Amboseli ecosystem select areas with different grass heights. He then concluded that if the animals are responding to grass height, then a changing spatial pattern would lead to changes in their habitat selection and hence distribution. Attwell (1977) showed a similar trend with the four major grazing ungulates in the Hluhlwe Game Reserve where mean height of the herbaceous layer depicted high discriminatory powers in their habitat choice. Duncan (1975), on the other hand, showed that the proportion of green leaf had profound effects on the quality of the diet of Topi by overriding the importance of grass height. Herbivores therefore tend to select areas based on both the floristic and structural features of the habitat.

The final aim of this chapter is to isolate those floristic and structural components of the grassland to which the habitat selection of the Pilanesberg grazers (especially the white rhino) are most closely related. This will not only give an insight into the causes of habitat selection and movement, but ultimately provide the information needed to estimate herbivore stocking densities in the reserve.

4.2 Materials and Methods

4.2.1 Field Measurements

The methods are broken up into three sections; the first concerns the calculation of habitat preferences using the road transect data, the second the measurement of the foraging sites, and the third the dietary selection within them.

4.2.1.1 Habitat Preferences of the Herbivores

The field data required to analyze habitat preferences were obtained from the road transects mentioned earlier in chapter three. Each transect shown in Figure 3.1 was driven once every morning between 06h00 and 09h00. When an animal was sighted the habitat in which it was present was identified using the classification described in the previous chapter. Each observation could then be related to one of the six possible plant communities; secondary grasslands, pediment grasslands, valley savannas, hillside savannas, Acacia and riverine thickets or Cynodon dactylon "lawns identified in chapter three.

4.2.1.2 Feeding Site Descriptions

The herbivores were located by vehicle and observed feeding for at least fifteen minutes. This ensured that the animals exerted a reasonable grazing pressure on the herbaceous vegetation, and that accurate boundaries around the site could be delimited. A total of 113 feeding sites was recorded, 75 for rhino (all seasons), 12 for hartebeest (dry season), 15 for impala (dry season), and 7 for zebra (dry season). It should be noted that only 4 impala sites were recorded, but have been included in the analyses because of the high density of this species in the reserve. The impala are extremely alert and seldom feed in a particular site long enough for it to be clearly demarcated.

The number of quadrats (0,25 sq. m.) positioned in each site depended largely on the feeding site areas, which could vary from 25 to 1000 square metres. In each quadrat the following site characteristics, (except grass height), were estimated using the eight point scale described by Anderson and Walker (1974) and Walker (1976);

1. Cover and abundance of the herbaceous vegetation. This estimates the amount of rooted basal and aerial cover of the herbaceous layer.
2. Height, which is the average height of the green grass cover to the nearest 10 cm and averaged for all the quadrats.
3. Proportion of forbs making up the herbaceous layer.
4. Litter, which is the dead and broken plant material in contact with the soil surface.
5. The proportion of moribund grass. This is the dead plant material older than one year which is not in contact with the living material.
6. Soil capping which may be either clay or algal capping.
7. Erosion. (Surface or sheet erosion).
8. Grazing or the proportion of the biomass of the sward consumed by the grazers. This was subjectively estimated for each grass species in the quadrats.

The above measures were then averaged for each variable according to the formula developed by Walker (1976);

$$(n_i \times c_i) / N \quad \ldots\ldots\ldots\ldots 4.1$$

where, n_i is the number of quadrats in rank i,

c_i is the class midpoint of rank i,

N is the total number of quadrats.

The herbaceous species composition was determined using the bulk contribution method described in the previous section.

It should be noted that factors 3,4,5,6, and 7 were not used in the final analysis as they appeared to play only a minor role in habitat selection - only minor differences in these variables were apparent between sites.

In order to obtain a measure of the woody vegetation the trees within a defined area around the feeding site were divided into two categories; those with a canopy height greater than two metres and those below two metres. The former provides an indication of the importance of shade, and the latter the importance of lateral cover. The measurements of these two categories were recorded as follows;

1. All the trees with canopies below 2 metres were recorded as a percentage of the total canopy cover over the whole area.

2. Trees with canopies below 2 metres were ranked from 1 to 5 depending on their diameters. Their respective frequencies were then noted. The 5 point rank was based on the following scale;

RANK	DIAMETER(m)
1	0.0 - 0.5
2	0.6 - 1.0
3	1.1 - 1.5
4	1.6 - 2.0
5	> 2.0

A "lateral cover index" was calculated, using the frequency data for each rank, as follows:

$$\text{Lateral Cover Index (LCI)} = \sum_{i=7}^{5} (A_i \times RF_i) / TLA \ldots\ldots 4.2$$

where, RF_i is the relative frequency of the 5 class types, i, TLA is the total lateral area determined by assuming that the site is bounded by a 'fence' 2m high with a lateral area of Height(2m) X Width X Length, and

A_i is the lateral area covered by all the size classes. The following formula is used to calculate the lateral area of a tree which is assumed to be a semi-circle;

$$\text{Area } (A)_i = (\pi r_i^2) / 2 \quad ....4.3$$

where r is the radius of the tree's canopy.

The trees below 2 m were regarded as semi-circles from the ground surface as it was felt that lateral cover would otherwise have been overestimated if the trees were regarded as circular. The values of LCI range from 0 to 1.

By using the above information the relationship between the herbivore species and their selection for certain grassland factors will become apparent.

In addition, the proportional contribution of each grass species to the herbaceous layer in each site was recorded. Table 4.1 lists all the habitat variables which are thought to influence the distribution and habitat selection of the grazing herbivores.

4.2.1.3 Diet

The diet of the herbivores was obtained by estimating the proportional use of each freshly grazed grass species in each quadrat. This method was preferred to the other techniques e.g. stomach content analyses (e.g. Sinclair and Gwynne, 1972; Gwynne and Bell, 1968) and dung analyses (Storr, 1961; Stewart, 1965, 1967; Monro, 1982) for the following three reasons;

1. stomach contents of the grazers, especially the white rhinos, were seldom attainable,
2. dung analyses have resulted in limited success because of

Table 4.1 : Key to the 35 Habitat Factors used in the Correspondence Analysis

Mnemonic	Habitat Factor
CCA	Canopy cover (0 to 10%)
CCB	" " (11 to 40%)
CCC	" " (41 to 100%)
LCA	Lateral cover index (0.0 to 0.1)
LCB	" " " (0.2 to 0.4)
LCC	" " " (0.5 to 1.0)
HCA	Herbaceous cover (0 to 30%)
HCB	" " (31 to 50%)
HCC	" " (51 to 100%)
HEA	Average grass height (0 to 5cm)
HEB	" " " (6 to 15cm)
HEC	" " " (greater than 15cm)
CYDA	*Cynodon dactylon*
ARCO	*Aristida congesta*
RHRE	*Rhynchelytrum repens*
HECO	*Heteropogon contortus*
THTR	*Themeda triandra*
ERCU	*Eragrostis curvula*
ERSU	*E. superba*
ERRI	*E. rigidior*
ERGU	*E. gummiflua*
UNPA	*Unpalatable* species, eg. *Elyonuris argenteus*, and *Cymbopogon* species
HYHI	*Hyparrhenia hirta*
BOIN	*Bothriochloa insculpta*
BRSE	*Brachiaria serrata*
URMO	*Urochloa mosambicensis*
LOFL	*Loudetia flavida*
DIER	*Digitaria eriantha*
PADE	*Panicum deustum*
PACO	*P. coloratum*
POSQ	*Pogonarthria* sqarrosa
SPPY	*Sporobolus pyramidalis*
CHVI	*Chloris virgata*
SENI	*Setaria nigrirostris*
ERCU	*Eragrostis* species

differential digestion (eg. Stewart and Stewart, 1970), and

3. most importantly, dietary selection coefficients cannot be calculated without information on the availability of the grass species presented to them. With the transect method both availability and utilization of each grass species can be estimated.

The percentage contribution of each grass species in the herbivores' diet was estimated using the following formula developed by Taylor and Walker (1978);

SEE 82

$$D = C \times A \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 4.4$$

where, C is the percentage utilization, and
A is the percentage bulk contribution in the feeding site.

The dietary selection or preference by each herbivore for a particular grass species, was calculated as follows;

$$P = C / A \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 4.5$$

The grass species utilized by the herbivores were then categorised into 3 different forage types based on their dietary importance; palatable, intermediate and unpalatable. (See section 3.3.1).

4.3 Data Analysis

4.3.1 Calculation of the Habitat Preferences Indices

The habitat preferences were determined for white rhino, hartebeest, wildebeest, zebra and impala by recording the percentage time spent foraging in each of the major habitat types.

The selectivity of the ungulate species (Xi) for a vegetation type j was described by calculating the "comparative grazing intensity" (Hunter, 1962) which quantifies any preferences shown by the herbivores.

Xi Pref. = % of species Xi in veg. type j / % of total area in reserve covered by veg. type j along each transect 4.6

The values of selectivity using this equation can in theory, range from zero to infinity (Duncan, 1975). When a value exceeds one then selection for the vegetation type is occurring, when less than one, negative selection and when equal to one, random selection. The percentage area of each vegetation type seen along the road transects (using figures 2.6 and 3.1) are given below;

(i) Secondary grassland - 19.6%,
(ii) Pediment grassland - 6.0%,
(iii) Valley savanna - 27.6%,
(iv) Hillside savanna - 39.3%
(v) Thickets - 6.5%, and
(vi) <u>Cynodon</u> <u>dactylon</u> "lawns" - 1%.

Duncan (1975) has however identified a number of disadvantages using this method. Firstly, no standard errors can be attached to the values, although the significance of departures from 1 (i.e. random or no selection) can be tested using the chi- square tests. Secondly, the visibility or animal detectability may differ for each habitat type. The second problem is probably the most serious of the two in that biases for or against animal sightings differ depending on the densities of the woody vegetation in each habitat type. The animal detection coefficients should therefore be estimated separately for each habitat type and also for each season. Unfortunately, the importance of these coefficients was only realized (Peddie, pers com) after the field studies had been terminated. The habitat preference data should therefore be analyzed with caution, although the relative importance values of each habitat type to a particular species are believed to be correct.

What these results do not tell us however, is why the species select for particular habitat types. The next section therefore describes a technique - namely Correspondence Analysis - which is used to identify the underlying factors governing the relationship between the herbivore species and their environment Beardall (1982).

4.3.2 Interrelationships Between Habitat Selection and Grassland Structure

The environment is a very complex system comprising of a number of features, both vegetation and physiographic. Because of this a multivariate technique is used to display the importance of each environmental factor to a herbivore species (Beardall, 1982).

Beardall (1982) analysed the use of three similar multivariate techniques, ie. Correspondence Analysis, Principal Component Analysis and Linear Logistic Model on a two- dimensional data matrix consisting of animal species measured over a range of habitat factors. These methods use graphical techniques based on an eigenstructure approach to represent multivariate data in a multi-dimensional space (Beardall, 1982). By interpreting the output in terms of the habitat factors, ecological meaning with regards to the species-environment relationship can be given to the orthogonal axes. Beardall (1982) concluded that of all the analyses, Correspondence Analysis is best suited to ecological data even though similar results were obtained by all the analyses. The suitability of this technique is highlighted by the fact that a simultaneous graphical display of the observations (herbivore species) and the variables (habitat factors) is obtained. Hence Correspondence Analysis was used to identify those structural features of the habitat which influenced the selection by grazing ungulates at Pilanesberg.

4.3.2.1 Correspondence Analysis

Correspondence Analysis is used to display graphically the relationship between the subjects and objects of a matrix of non-negative numbers, simultaneously (Beardall,1982) The model that she used follows that of Greenacre (1978) and is briefly described below.

The elements of the data matrix are first transformed to proportions that may be interpreted as probability values. This new matrix (P) is then tested using an approach similar to the chi-squared statistic for independency of the rows (ie. species) and columns (habitat variables). In order to test this hypothesis the matrix P must first be transformed into a notation such that,

$$P_{ij} = P_{ij} - r_i cj^T \text{ ....4.7}$$

where, r_i is the sum of row i of P, and

c_j is the sum of column j of P.

The next step involves the "centering" of the matrix where, rc^T is the mean or "centre" of the rows and columns of P. Thus by subtracting this term from the matrix P we merely "move" the matrix so that it "centres" on the origin. This transferred matrix has been termed the "deviation score" matrix.

The elements of the subjects and objects measured on these disparate scales are then differentially weighted and "equalised" by dividing each element by the square root of the row and column sums. Finally, the coordinates of the subjects and objects in a k- dimensional space are calculated using both the eigenvalues and the diagonal matrices of the row sums and the column sums.

In Correspondence Analysis the principle axes are chosen so as to maximize what is termed the "Inertia". The inertia can be considered as a measure of dispersion of the points in space. Thus Beardall (1982) defined a correspondence analysis as the "identification of a subspace (cloud of points of subjects and objects) along which the inertia is a maximum (i.e. the eigenvector associated with the largest eigenvalue)". The second axis is that axis orthogonal to the first along which the inertia is also a maximum, and so on for the third and fourth axes.

To summarise, the rows and columns of a data matrix are represented by two clouds of points in a multi-dimensional space. The inertia of these clouds can be considered as a measure of dispersion or spread of these points, taking into account both their distance and their attributed masses (ie. the proportion of the contribution that a subject makes on the whole sample).

Correspondence Analysis thus provides a visual interpretation of the relative position of both these clouds in a common subspace of low dimension (Beardall, 1982). To get an idea of how close the subjects and objects are to each other, one measures the angle that the two points make to each other when joined to the origin. The smaller the angle, the closer they are related. An "Importance Index" was calculated by first dividing this angle by 180 and then subtracting from one. The values therefore range from 0 (no relatedness or avoidance) to 1 (closely related or high preference). Therefore, by measuring the angles between the points of the herbivores and the habitat factors, information can be collected on the relatedness of the two, ie. the importance of particular habitat factors on the herbivore's habitat selection.

The rows in the matrix represent the herbivore species and the columns, the habitat factors. The entries in the matrix represent the frequency of occurrence of a certain species with a particular habitat factor (see Table 4.1).

The computer program used for the analysis was written in FORTRAN by Beardall (1982).

4.4 Results and Discussion

4.4.1 Seasonal Changes in Habitat Selection

The annual cycle was divided into four seasons; Early-wet (October to December), Late-wet (January to April), Early-dry (May to July) and Late-dry (August to September).

Petrides (1956), Darling (1960), Vesey-Fitzgerald, Blankenship and Field (1972), Pienaar (1974), Ferrar and Walker (1974) and others have all identified vegetation as the all-important factor governing herbivore distributions. The seasonal changes in habitat selection were therefore analysed for all species. Figures 4.1 to 4.5 show the seasonal changes in habitat selectivity for the five major wild ungulates.

The habitats considered here are the major vegetation types defined in section 3.3.1. They were based largely on topography, tree density, successional stage and the percentage bulk contribution of the grass species.

This section attempts to identify, firstly, which habitats were preferred by the Pilanesberg grazers, and secondly, what environmental factors influenced their selection.

4.4.1.1 White Rhinoceros

Based on the data collected from the road strip transects, the white rhinos showed a marked seasonal change in habitat preference (refer to Appendix B), especially between the secondary grasslands, valley savannas, thickets and <u>Cynodon dactylon</u> lawns (figure 4.1). During the wetter months there was a high preference for the secondary grasslands ($p < 0.001$, Chi-square test), whereas during the drier seasons the more wooded valley savannas and thickets were selected ($p < 0.001$, Chi-square test). There were no marked seasonal differences in their selection for the pediment grasslands ($p > 0.1$, Chi-square test). Negative selection, ie. avoidance, was observed for the hillside

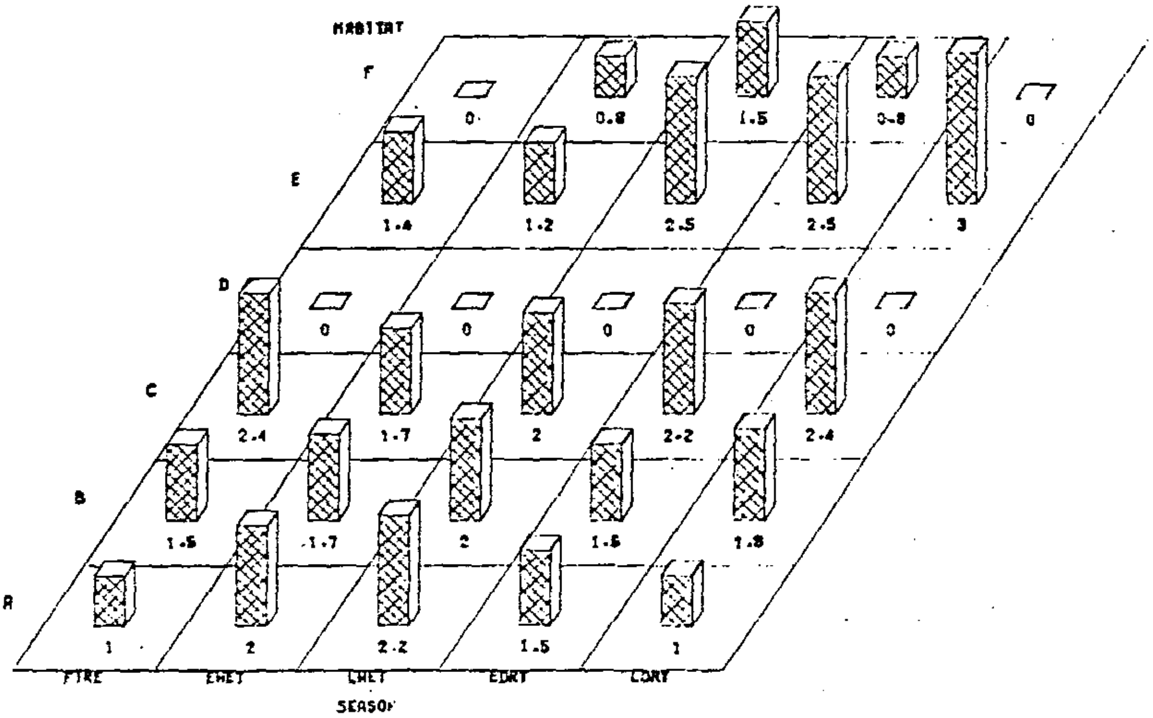


Figure 4.1 : Seasonal patterns of habitat selection by the White Rhino in the Pilanesberg Game Reserve. (A = Secondary grassland; B = Pediment grassland; C = Valley savanna; D = Hillside savanna; E = Thickets; F = *Cynodon dactylon* "lawns" and termitaria; FIRE = Veld fire; EWET = Early-wet; LWET = Late-wet; EDRY = Early-dry; LDRY = Late-dry).

savannas. This probably results from their inaccessibly steep slopes.

As shown in Figure 4.1, selection for the thickets was prevalent throughout the entire year except for the early-wet and fire periods which showed only a slight positive selection. These results may unfortunately underestimate the rhino's selection for the denser areas, eg. thickets because of the poorer visibility. This would therefore create a bias against the selection for these habitats. The incorporation of "visibility" or "detectability" coefficients in the equation used to calculate Preference Indices (equation 4.6) would alleviate this problem.

The white rhinos therefore generally selected for the relatively shorter grasslands (eg. the heavily utilized thickets and Cynodon "lawns") during the wetter periods when grass production and nutritional values were at their highest. The Cynodon dactylon "lawns" and termitaria (accounting for less than 2% of the reserve) were utilized frequently, particularly towards the end of the wet season. Similar results were found in the Umfolozi Game Reserve by Owen-Smith (1973).

It is interesting to note how the presence of a fire affects the herbivore distribution and habitat selection. Significant differences in habitat selection occurred between the fire and the other seasons ($p<0.001$, Chi-square tests). The importance of any particular habitat tends to decrease with the presence of a green flush after a burn, ie. habitat selection tends to be more random.

These "megaherbivores" (Owen-Smith, 1981) therefore tend to behave as habitat generalists by utilizing a wide range of habitat types, both on an annual, and seasonal basis. Five out of the six habitats were positively selected for at least once during the year.

This generalistic behaviour may therefore imply one of two possibilities. Firstly, these animals may require a high habitat diversity in order to survive in this reserve; or secondly, because of their "plastic" or generalistic foraging behavior, the white rhinos are able to survive in either one of the habitat types. The importance of either of these possibilities becomes apparent when estimating carrying capacities in the reserve. The relationship between diet and habitat selection may provide an indication as to which possibility is most likely. For instance, if dietary selection, which changes seasonally, is closely related to the habitat type then the first possibility is most likely. However, if their dietary selection differs little seasonally, but seasonality is shown in habitat selection then the latter is most likely.

4.4.1.2 Hartebeest

The hartebeest, in contrast to the white rhinoceros, behaves largely as a habitat specialist, specializing almost exclusively on the secondary and pediment grasslands and to a lesser extent valley savannas. Seasonal variation in their habitat selection was apparent for most of the habitats with marked differences between the wet and dry seasons (see Appendix B and Figure 4.2). The hartebeest also showed a high selection for the valley savannas during the early-wet season. Positive selection for both the pediment and secondary grasslands occurred throughout the entire year, although their importance does tend to drop during the drier months. The hillside savannas however, were negatively selected throughout most of the year, but showed a greater importance during the drier months. The hartebeest also tend to move up on the slopes during the early- and late-dry seasons when the selection for the secondary grasslands drops.

No selection was observed for the <u>Cynodon</u> <u>dactylon</u> "lawns" or termitaria.

4.4.1.3 Wildebeest

Significant differences in the wildebeest habitat selection was shown throughout the entire year (refer to Appendix B) again

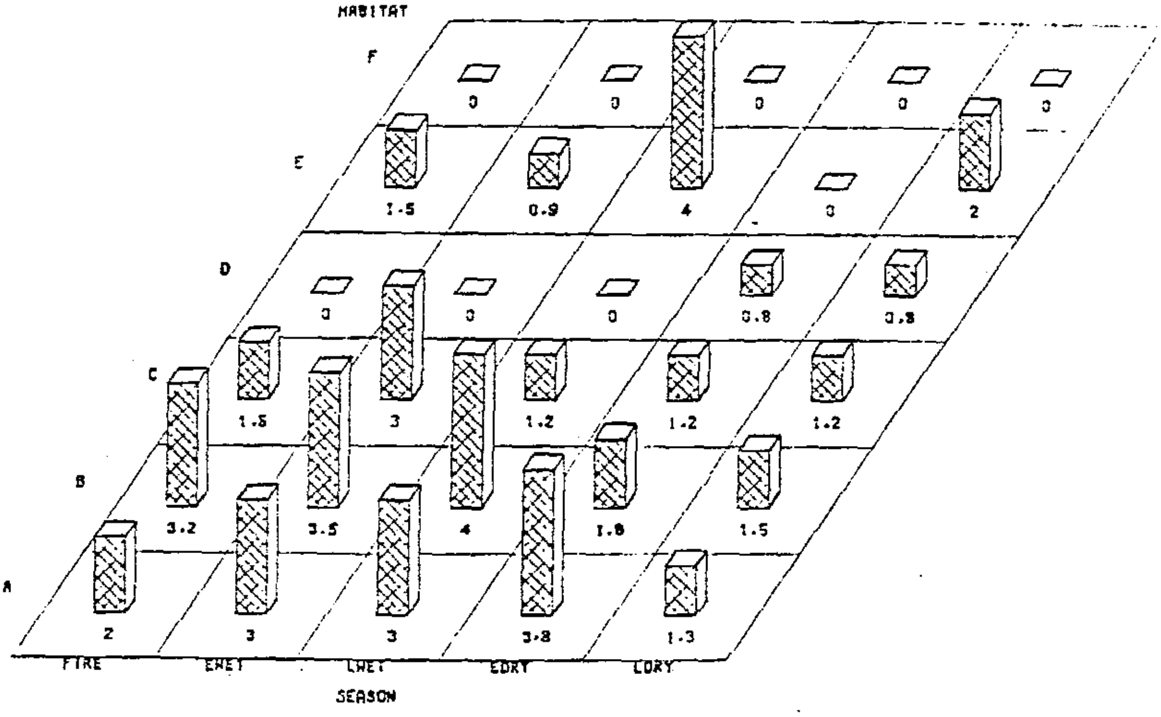


Figure 4.2 : Seasonal patterns of habitat selection by the Hartebeest in the Pilanesberg Game Reserve. (A = Secondary grassland; B = Pediment grassland; C = Valley savanna; D = Hillside savanna; E = Thickets; F = *Cynodon dactylon* "lawns" and termitaria; FIRE = Veld fire; EWET = Early-wet; LWET = Late-wet; EDRY = Early-dry; LDRY = Late-dry).

indicating a generalistic feeding behaviour similar to that of the white rhino. A positive selection for all habitats except the hillside savannas and Cynodon dactylon "lawns" was apparent (Figure 4.3). A high preference was shown for the secondary grasslands, valley savannas and thickets throughout the year. However, there was a greater tendency for the wildebeest to select the valley savannas during the latter part of the dry season. Slight seasonal changes occurred in their selection for the Acacia and riverine thickets with a greater preference shown during the late-wet and late-dry periods.

Witkowski (1983) was able to show that the wildebeest in the Klaserie Private Nature Reserve selected both the Acacia and riverine vegetation more than any other vegetation type. The density of the wildebeest in these vegetation types relative to the other habitats was approximately six times greater. He attributed these preferences to the high proportion of palatable short-grass species such as Digitaria eriantha and Urochloa mosambicensis. Similarly, Attwell (1977) found that the Acacia nigrescens open woodland and the A. karroo and A. caffra thickets were most favoured by wildebeest in the Umfolozi Game Reserve. These habitats were dominated by either Panicum maximum, Themeda triandra or Cyperus textilis. Hirst (1975) found that in the Timbavati reserve in the Transvaal, the wildebeest were most often associated with "open short-grass savannas". Other habitats which were frequently utilized by the Timbavati population included the "wooded short- and tall-grass savannas" and the sparsely wooded "grass / forblands".

Similar results were obtained in the Pilanesberg Game Reserve where the more palatable species such as Heteropogon contortus, Rhynchyletrum repens and Themeda triandra are present in both the secondary grasslands and valley savannas. The relationship between habitat selection and diet is discussed in section 4.3.3.

4.4.1.4 Zebra

Figure 4.4 and Appendix 3 show the seasonal changes in the

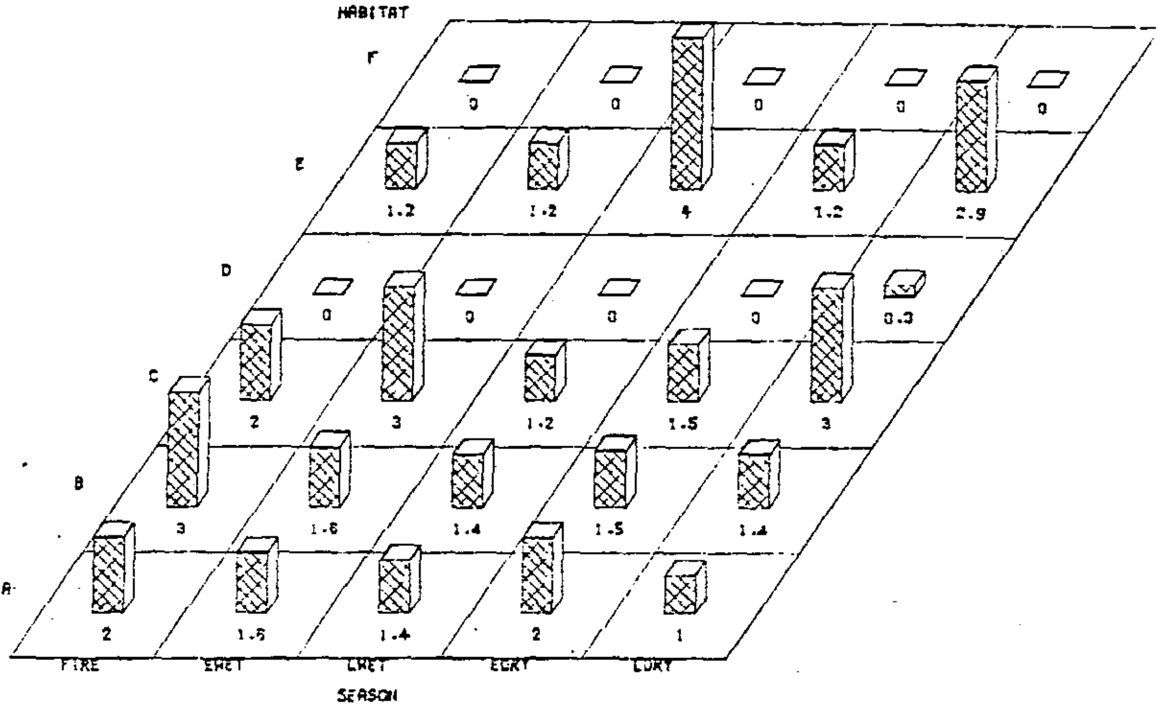


Figure 4.3 : Seasonal patterns of habitat selection by the Wildebeest in the Pilanesberg Game Reserve. (A = Secondary grassland; B = Pediment grassland; C = Valley savanna; D = Hillside savanna; E = Thickets; F = Cynodon dactylon "lawns" and termitaria; FIRE = Veld fire; EWET = Early-wet; LWET = Late-wet; EDRY = Early-dry; LDRY = Late-dry).

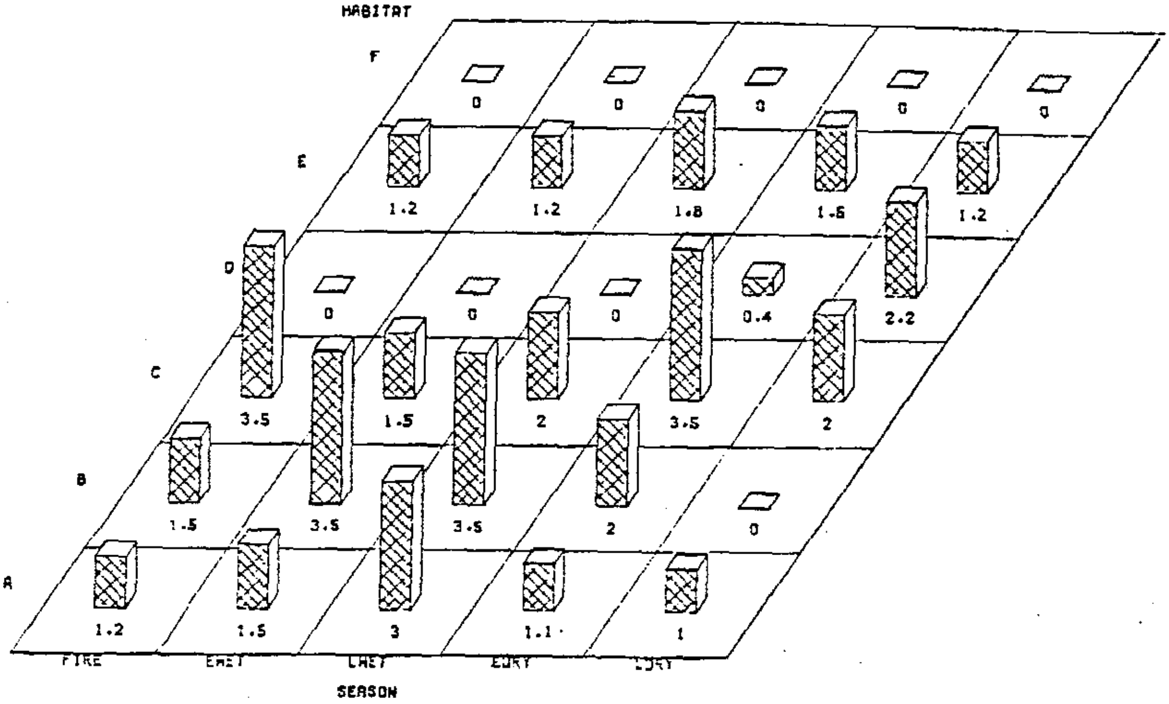


Figure 4.4 : Seasonal patterns of habitat selection by the Zebra in the Pilanesberg Game Reserve. (A = Secondary grassland; B = Pediment grassland; C = Valley savanna; D = Hillside savanna; E = Thickets; F = *Cynodon dactylon* "lawns" and termitaria; FIRE = Veld fire; EWET = Early-wet; LWET = Late-wet; EDRY = Early-dry; LDRY = Late-dry).

preferences for the six major habitat types by the zebra. There was generally a high positive selection for the secondary grasslands, valley savannas and pediment grasslands throughout most of the year. There was also a slight tendency for the zebra to select positively for the Acacia and riverine thickets especially during the late-wet seasons. It was also interesting to note the sudden positive selection for the hillside savannas during the late-dry season. There was thus a movement up the slopes when the forage in the valley bottomlands decreased as a result of heavy grazing during the wetter months. Selection for all the habitats dropped during the dry season, especially the late-dry season.

Because of their less efficient mode of digestion, zebra require a relatively greater quantity of plant biomass than ruminants of the same body weight, eg. wildebeest (Hofmann and Stewart, 1972). They therefore select habitats with tall grasslands with high plant biomasses, such as the valley and hillside savannas. During the latter part of the dry season a high percentage of the plant biomass in the bottomlands had been utilized, thus explaining the movement of zebras up the slopes. They may have therefore been "forced" to use this vegetation type in order to obtain adequate forage to survive during this stressful period.

4.4.1.5 Impala

The impala were included in this study for two reasons; firstly, because of their relatively high densities, and secondly, because of their ability to maintain these high densities under adverse environmental conditions (Dassman and Mossman, 1962). Although, this species is classed as an intermediate or mixed feeder, ie. it alternates from a browsing to a grazing habit, its high densities do have a heavy impact on the habitat and its condition.

Their most preferred habitats were, firstly, the Acacia and riverine thickets, and secondly, the valley savannas (Figure 4.5 and Appendix B). The impala showed a negative selection for the

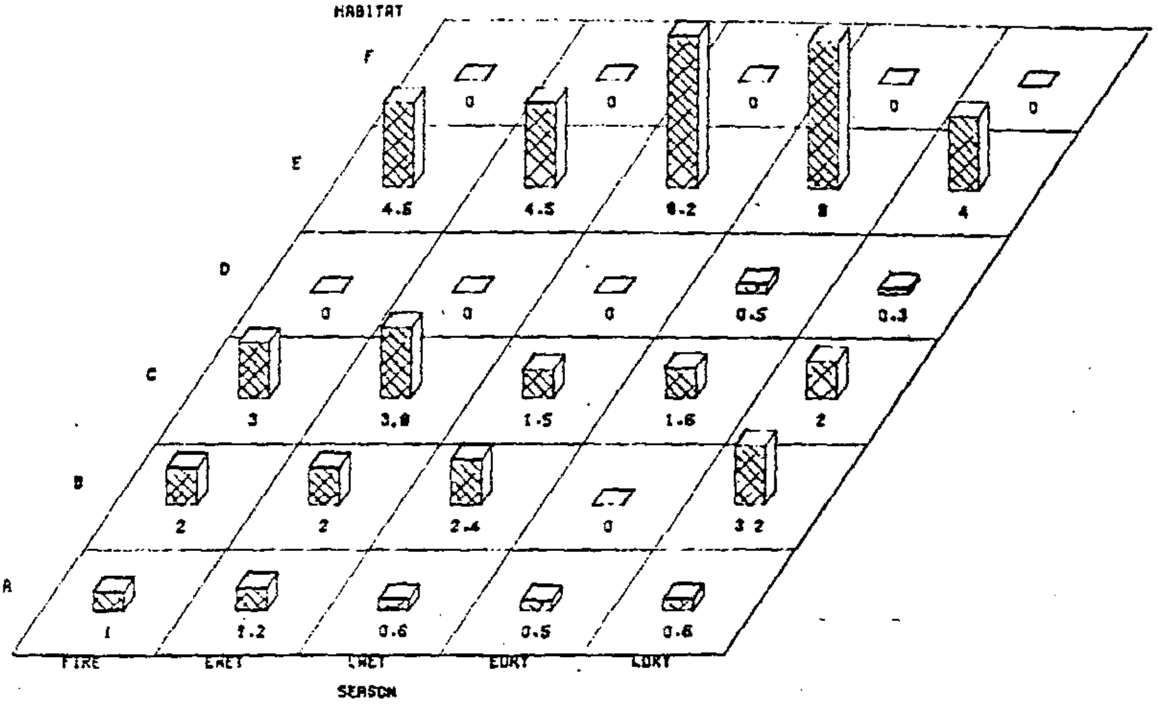


Figure 4.5 : Seasonal patterns of habitat selection by the Impala in the Pilanesberg Game Reserve. (A = Secondary grassland; B = Pediment grassland; C = Valley savanna; D = Hillside savanna; E = Thickets; F = *Cynodon dactylon* "lawns" and termitaria; FIRE = Veld fire; EWET = Early-wet; LWET = Late-wet; EDRY = Early-dry; LDRY = Late-dry).

hillside savannas throughout the entire year, and for pediment grasslands only during the early-dry season.

Figure 4.5 shows a slight alternate selection between the thickets and the valley savannas. The Acacia and riverine thickets were preferred during the late-wet and early-dry seasons, with higher preferences shown for the valley savannas during the early-wet seasons. This seasonal pattern may be either a result of their mixed diet or their ecotonal preference. Taylor and Walker (1978) in the Zimbabwe lowveld found that the impala preferred the riverine fringe followed by the Acacia - Spirostachys tree savanna. Goodman (1975) and Dunham (1980) in the Sengwa wildlife research area in northwest Zimbabwe also found impala preferring the riverine fringe, particularly in the dry season. Movement into the Colophospermum mopane woodland occurred during the wet season. Similar results were found by Witkowski (1983) in the Klaserie Private Nature Reserve.

4.4.2 Relationship Between the Herbivores and Habitat Factors

This section attempts to isolate those habitat factors which play an important role in determining habitat selection by the herbivores. It has become apparent in a number of studies (eg. Ferrar and Walker, 1974; Attwell, 1977) that herbivores select for certain microhabitat factors when feeding.

In order to extract those variables influencing the herbivores' habitat selection, the frequency scores of the herbivore species for each of the 35 habitat factors were used (Table 4.2). The information output retained by the computer will be first explained, and then the results interpreted.

Table 4.3 gives the breakdown of the inertia (ie. the dispersion of the points in space) for each axis or factor. Those axes which contribute the most to the scattering have higher eigenvalues. The total inertia (I), is calculated as the sum of the moments of inertia for each axis (Beardall, 1982). Each eigenvalue is expressed as a percentage of the total inertia

Table 4.2 : Frequencies of Association of the 5 Herbivore Species with each of the 35 Habitat Factors. A key to Habitat Factors is given in Table 4·1 (n = Total number of observations).

	Canopy									Grass Height			Grass Species							
	Canopy			Lateral			Herbaceous													
SPECIES	CCA	CCB	CCC	LCA	LCB	LCC	HCA	HCB	HCC	HEA	HEB	HEC	CYDA	ARCO	RHRE	HECO	THTR	ERCU	ERSU	ERRI
White rhino:Fire	1	5	1	4	2	1	1	2	3	2	4	1	6	5	3	4	2	2	3	3
Early wet	18	6	0	21	4	0	1	7	17	8	18	0	19	10	9	19	5	13	15	17
Late wet	5	8	5	12	3	3	0	2	16	3	14	0	14	6	2	8	2	10	9	8
Early dry	12	6	5	11	9	3	1	2	20	1	17	5	20	18	12	22	10	16	8	16
Late dry	4	4	1	6	1	1	0	0	9	1	8	0	6	5	3	9	4	4	4	6
Wildebeest	11	3	2	14	2	0	1	0	15	1	10	5	14	13	9	11	4	15	7	8
Hartebeest	10	1	3	12	1	0	0	1	13	0	6	7	9	11	10	9	5	9	5	8
Zebra	2	5	5	8	0	0	0	0	8	0	6	2	2	7	5	7	6	2	3	1
Impala	1	0	3	2	2	0	0	2	2	1	3	0	3	3	0	2	1	4	1	4

Table 4.2 : (Cont.)

SPECIES	ERGU	UNPA	HYHI	BOIN	BRSE	URMO	LOFL	DIER	PADE	PACO	POSQ	SPPY	CHVI	SENI	ERCR	n
White rhino:Fire	0	2	3	0	2	0	0	2	0	0	0	0	0	0	3	9
Early wet	0	12	14	1	2	8	0	3	3	0	1	2	0	2	4	22
Late wet	0	4	4	3	1	14	0	3	11	2	0	4	5	1	5	16
Early dry	3	11	10	3	6	11	0	6	12	9	2	2	5	1	10	23
Late dry	2	5	8	0	5	4	0	3	5	4	2	0	1	0	4	10
Wildebeest	4	10	10	3	7	6	0	7	2	5	5	5	3	0	5	16
Hartebeest	5	10	11	0	7	4	1	6	0	3	6	0	1	2	5	12
Zebra	1	6	2	1	3	2	3	1	0	0	0	3	0	0	0	10
Impala	0	0	1	0	1	2	0	1	3	0	0	2	0	0	2	4

Table 4.3 : Moments of Inertia and their Percentage of the Total Inertia.

FACTOR	INERTIA (eigenvalue)	PERCENT	CUMUL. PERC.
1	0.0850	32.2	32.2
2	0.0541	20.5	52.7
3	0.0528	20.0	72.7
4	0.0227	8.6	81.3
5	0.0199	7.5	88.8
6	0.0122	4.6	93.4
7	0.0094	3.6	97.0
8	0.0080	3.0	100.0

(column PERCENT) and the cumulative percentages of inertia are listed in the column headed CUMUL. PERC.

The program then calculates the decomposition of the moments of inertia for the subjects and the objects, respectively (Tables 4.4 and 4.5). In other words, it calculates the contribution that both the subjects (herbivores) and objects (habitat factors) make on each axes' inertia (see below).

From Tables 4.4 and 4.5 the following information can be extracted, based on Beardall (1982);

(i) For each point the mass (defined as the proportion of the contribution that each subject makes on the whole sample) and inertia are given in the columns headed MASS and INR, respectively.

(ii) For each moment of inertia and corresponding principle axis the coordinate of the point on the axis (column headed F), and the relative contribution in the column headed CTR, are given.

(iii) The cosine squared of the angle that the point makes with this subspace is given in the column headed QLT. Beardall (1982) has defined this value as the quality of each point's representation in the subspace of the first three axes. It is calculated as the sum of the relative contributions of these axes.

From Table 4.3 it can be seen that 72.7 percent of the inertia is accounted for by the first 3 moments of inertia. Thus, only the first 3 axes are considered.

By analyzing Tables 4.4 and 4.5 in conjunction with the graphical display (Figure 4.6), interpretations can be made so as to relate the herbivore feeding sites to particular habitat factors. It should be noted that the axes are so orientated as to account for maximum inertia (or scattering) in the ordination space. Thus, the values under columns COR - the contribution of the axis to the inertia of the subjects or objects - and those in

Table 4.4 : Decomposition of the first 3 Moments of Inertia in terms of the Herbivore Species and Seasons (subjects).

NAME		QLT	MASS	INR	1 F	COR	CTR	2 F	COR	CTR	3 F	COR	CTR
White rhino:	Fire	997	45	78	119	31	8	-248	138	52	-164	60	23
	Early wet	998	170	154	160	107	52	-283	336	252	-347	507	391
	Late wet	996	127	152	464	684	324	53	8	7	213	144	111
	Early dry	996	208	66	57	39	8	200	475	154	80	77	26
	Late dry	996	81	51	-27	4	1	175	184	46	1	0	0
Wildebeest:	Dry	995	148	70	-231	336	80	138	152	53	-37	11	4
Hartebeest:	Dry	997	123	137	-481	790	338	107	39	27	-111	42	29
Zebra:	Dry	997	62	199	-392	183	113	-595	420	408	575	390	391
Impala:	Dry	995	31	90	455	272	77	11	0	0	207	56	26

Table 4.5 : Decomposition of the first 3 Moments of Inertia in terms of the Habitat Factors (objects). See Table 4.1.

	NAME	QLT	MASS	INR	1 F	COR	CTR	2 F	COR	CTR	3 F	COR	CTR
1	CCA	995	43	25	-86	48	4	-38	9	1	-311	632	80
2	CCB	996	25	44	217	104	14	-348	269	58	221	107	24
3	CCC	997	17	53	30	1	0	-198	48	12	764	712	189
4	LCA	996	61	18	-43	25	1	-218	623	55	-66	58	5
5	LCB	996	16	25	394	374	30	162	63	8	-23	1	0
6	LCC	997	5	27	709	384	32	367	103	14	390	116	16
7	HCA	995	2	15	105	7	0	-209	30	2	-511	180	14
8	HCB	996	10	49	606	308	47	-496	207	50	-510	219	54
9	HCC	995	70	5	-10	5	0	-17	14	0	67	205	6
10	HEA	996	11	45	641	396	56	-526	267	60	-569	313	72
11	HEB	997	58	11	182	631	23	-103	206	12	23	9	1
12	HEC	996	13	47	-827	741	110	215	49	12	89	8	2
13	CYDA	997	63	13	165	494	20	30	16	1	-129	309	20
14	ARCO	997	53	12	-158	404	16	-24	10	1	75	89	6
15	RHRE	996	36	21	-348	759	52	-75	36	4	-67	28	3
16	HECO	996	62	11	-11	2	0	-77	131	7	-36	30	2
17	THTR	996	26	22	-241	261	18	-174	137	15	235	247	28
18	ERCU	996	51	13	57	44	2	122	208	14	-59	50	3
19	ERSU	995	37	15	165	242	12	-194	342	26	-161	235	19
20	ERRI	996	41	17	101	92	5	236	510	43	19	3	0
21	ERGU	998	10	33	-810	766	79	413	199	32	31	1	0
22	UNPA	996	41	17	-275	675	37	-124	138	12	-59	31	3
23	HYHI	996	43	21	-161	202	13	19	2	0	-273	576	61
24	BOIN	996	7	17	214	73	4	115	21	2	393	248	22
25	BRSE	995	23	26	-440	653	53	127	53	7	71	16	2
26	URMO	995	34	32	350	491	50	123	60	10	168	113	19
27	LOFL	996	2	88	-1424	237	65	-1806	382	165	1755	360	160
28	DIER	995	21	11	-209	327	11	209	324	18	-54	22	1
29	PADE	997	24	72	673	579	131	396	200	71	340	148	54
30	PACO	996	15	36	-176	50	6	676	736	133	119	22	4
31	POSQ	997	10	44	-802	595	83	484	216	47	-284	75	17
32	SPPY	997	12	40	181	37	5	-245	69	14	548	342	70
33	CHVI	994	10	29	332	144	13	562	414	60	361	170	25
34	SENI	996	4	13	-70	5	0	-71	5	0	-455	230	16
35	ERCR	997	25	14	109	79	4	264	466	33	-39	10	1

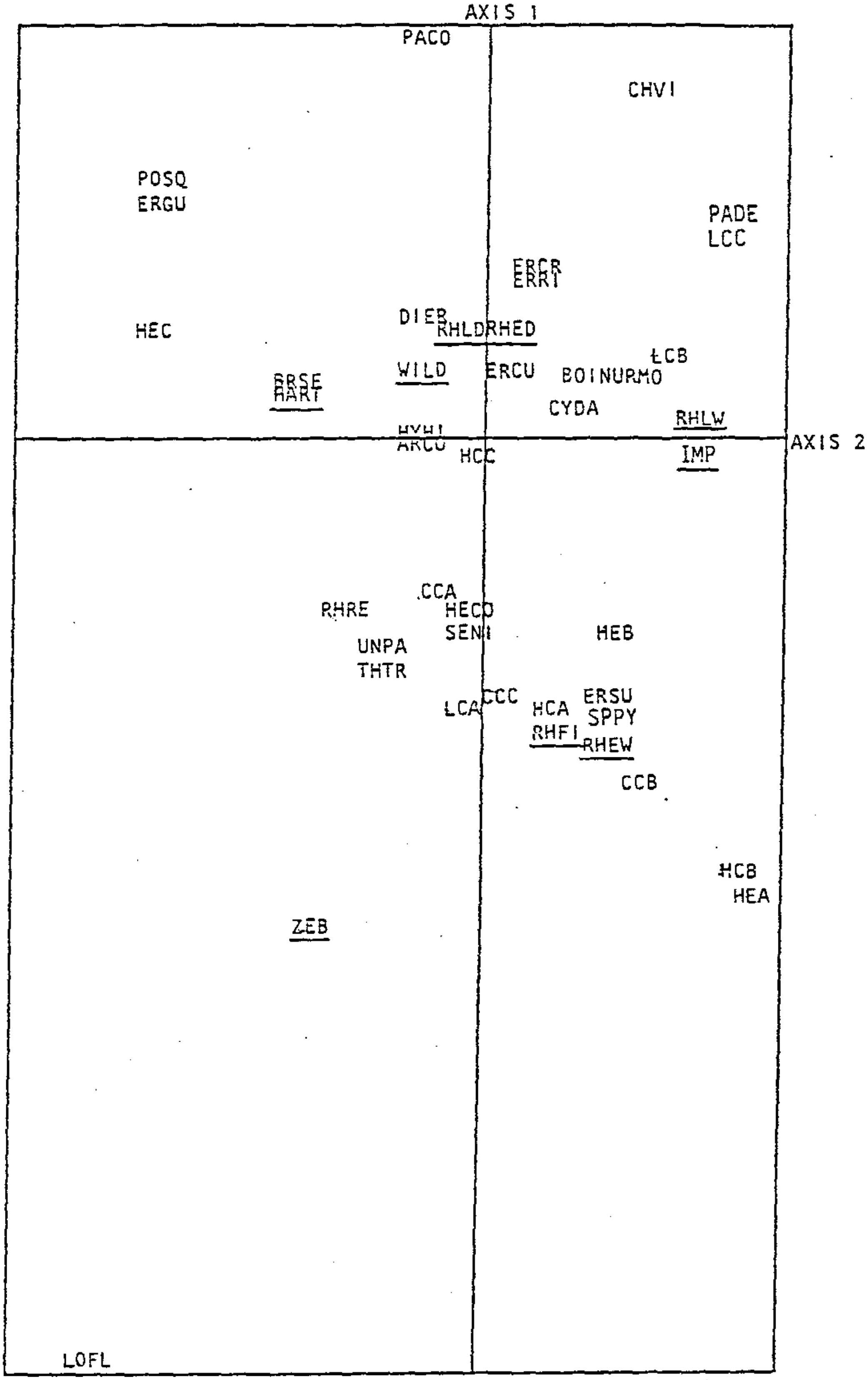


Figure 4.6 : Projections of herbivore species and habitat factors onto a plane of principal axes 1 and 2. A key to the species names and habitat factors is given in Appendix F.

column CTR - the contribution that the subject or object makes to the inertia of the axis - are important in the analysis (Beardall, 1982).

The first axis mainly separates zebra (ZEB) and *Loudetia flavada* (LOFL) from the rest which appear to be clumped into two groups. The one group is characterized by a medium (CCB) to high (CCC) tree canopy cover, low lateral cover (LCA), *Rhynchyletrum repens* (RHRE), *Themeda triandra* (THTR), unpalatable species (UNPA), *Setaria nigrirostris* (SENI) and *Heteropogon contortus* (HECO) and short (HEA) to medium (HEB) grass heights. This group is frequented only by white rhino during the fire (RHFI) and early-wet (RHEW) periods. These features relate to the more open savannas and pediment grasslands.

The second group, selected by the rest of the herbivores, is characterized by the more dense thickets and woodlands with high lateral cover (LCC) and low canopy cover (CCA). The herbaceous cover in these sites is also low relative to the other group. These sites are dominated by grass species such as *Cynodon dactylon* (CYDA), *Urochloa mosambicensis* (URMO), *Bothriochloa insculpta* (BOIN), *Eragrostis curvula* (ERCU), *E. rigidior* (ERRI), *Panicum deustum* (PADE), *P. coloratum* (PACO), *Chloris virgata* (CHVI), *Pogonarthria squarrosa* (POSQ), *E. gummiflua* (ERGU), *Brachyaria serrata* (BRSE), *Digitaria eriantha* (DIER), *Hyparrhenia hirta* (HYHI) and *Aristida congesta* (ARCO). This group appears to characterize a number of habitats ranging from *Cynodon dactylon* "lawns" to secondary grasslands, valley savannas and thickets. It also distinguishes between areas on the hillslopes and those in the valley bottomlands ranging from open grasslands and savannas to thickets.

The second axis contrasts white rhino, late-wet (RHLW), impala (IMP), white rhino, fire (RHFI) and white rhino, early-wet (RHEW) and habitat factors, short (HEA) to medium (HEB) grasslands, medium (LCB) to high (LCC) lateral cover, *Panicum deustum* (PADE) and *Urochloa mosambicensis* (URMO), with hartebeest (HART) and zebra (ZEB), and tall grasslands (HEC), *Eragrostis gummiflua*

(ERGU), *Brachyaria serrata* (BRSE) and *Loudetia flavada* (LOFL). This axis describes a gradient based on grass height, and lateral canopy cover.

Axis three (not displayed) contrasts white rhino, early-wet (RHEW) and white rhino, fire (RHFI) with zebra (ZEB) and white rhino, late-wet (RHLW). The habitat factors depict a gradient of short grasslands (HEA) with low (HCA) to medium (HCB) herbaceous cover, low canopy cover (CCA) and *Setaria nigrirostris* (SENI) to high canopy cover (CCC), *Loudetia flavada* (LOFL), *Sporobous pyrimedalis* (SPPY), *Bothriochloa insculpta* (BOIN) and *Chloris virgata* (CHVI).

Table 4.6 summarizes the output from this analysis by giving the "Importance Indices" of each habitat factor to the herbivore species. The index ranges from 0 (no preference or avoidance) to 1 (high preference). Thus the importance of each habitat factor to herbivore habitat selection can be analyzed.

Similar preferences were shown by the white rhino both after a burn, and during the early wet season. There is a high selection for short grasslands dominated by *Rhynchyletrum repens* (RHRE), *Heteropogon contortus* (HECO), *Themeda triandra* (THTR), *Eragrostis superba* (ERSU), unpalatable species (UNPA) and *Setaria nigrirostris* (SENI). These grasslands are typical of both the secondary grasslands and valley savannas classified in section 3.3.1. There is also a high preference for areas both of low (CCA) and high (CCC) canopy cover, suggesting that canopy cover probably plays a minor role during this period. There is however, a selection for habitats consisting of a low lateral cover index (LCA) and grass heights ranging from 0 to 10 cm (HEA). The structural feature, grass height therefore appears to play a major role in influencing white rhino habitat selection during the fire period.

During the late-wet season a greater selection is shown for the sites supporting the more palatable grass species, such as, *Cynodon dactylon*, *Eragrostis curvula* (ERCU), *E. superba* (ERSU),

Table 4.6 : Importance indices for each habitat factor by the herbivore species. A key to the habitat factors is given in Table 4.1

SPECIES	SEASON	Cover									Grass Height			Grass Species							
		Canopy			Lateral			Herbaceous													
		CCA	CCB	CCC	LCA	LCB	LCC	HCA	HCB	HCC	HEA	HEB	HEC	CYDA	ARCO	RHRE	HECO	THTR	ERCU	ERSU	ERRI
White rhino:	Fire	0.8	0.9	0.9	0.9	0.5	0.4	1.0	0.9	0.8	0.9	0.9	0.3	0.5	0.4	0.7	0.9	0.8	0.2	0.9	0.2
	Early wet	0.8	1.0	0.9	0.8	0.5	0.4	0.9	0.9	0.9	0.9	0.9	0.3	0.5	0.4	0.7	0.8	0.8	0.3	1.0	0.9
	Late wet	0.4	0.5	0.5	0.5	0.9	0.8	0.5	0.6	0.3	0.6	0.6	0.1	0.9	0.0	0.2	0.4	0.3	0.6	0.6	0.7
	Early dry	0.1	0.2	0.1	0.1	0.7	0.8	0.1	0.3	0.2	0.3	0.3	0.5	0.7	0.4	0.1	0.1	0.1	0.9	0.2	1.0
	Late dry	0.2	0.1	0.1	0.1	0.6	0.6	0.0	0.1	0.2	0.1	0.1	0.7	0.5	0.6	0.3	0.1	0.2	0.8	0.8	0.1
Wildebeest:	Dry	0.3	0.1	0.2	0.3	0.6	0.5	0.2	0.1	0.8	0.1	0.6	0.8	0.6	0.7	0.5	0.3	0.4	0.6	0.1	0.7
Hartebeest:	Dry	0.5	0.3	0.4	0.4	0.3	0.3	0.5	0.3	0.6	0.3	0.2	0.9	0.2	0.9	0.6	0.5	0.6	0.5	0.3	0.5
Zebra :	Dry	1.0	0.8	0.9	0.9	0.3	0.2	0.8	0.7	1.0	0.7	0.7	0.5	0.3	0.6	0.9	0.9	0.9	0.0	0.7	0.0
Impala :	Dry	0.4	0.6	0.5	0.5	0.8	0.8	0.6	0.7	0.3	0.6	0.7	0.1	0.5	0.0	0.3	0.5	0.4	0.6	0.6	0.7

Table 4.6 : (Cont.)

	ERGU	UNPAL	HYHI	BOIN	BRSE	URMO	LOFL	DIER	PADE	PACO	POSQ	SPPY	CHVI	SENI	ERCR
White rhino : Fire	0.2	0.8	0.4	0.4	0.3	0.5	0.8	0.1	0.4	0.1	0.3	0.9	0.3	0.9	0.3
Early wet	0.2	0.8	0.4	0.3	0.3	0.5	0.3	0.0	0.4	0.1	0.2	1.0	0.3	0.8	0.2
Late wet	0.2	0.3	0.1	0.8	0.1	0.9	0.3	0.3	0.8	0.5	0.3	0.6	0.6	0.4	0.6
Early dry	0.6	0.1	0.4	0.3	0.5	0.7	0.1	0.8	0.8	0.8	0.6	0.2	0.9	0.1	1.0
Late dry	0.8	0.2	0.6	0.6	0.7	0.6	0.2	0.9	0.7	0.9	0.2	0.1	0.8	0.1	0.8
Wildebeest	0.9	0.4	0.8	0.5	0.8	0.6	0.4	0.9	0.5	0.8	0.9	0.1	0.6	0.3	0.7
Hartebeest	0.9	0.6	0.9	0.3	0.9	0.2	0.6	0.7	0.3	0.6	0.8	0.3	0.4	0.5	0.5
Zebra	0.1	0.9	0.6	0.2	0.5	0.3	0.9	0.3	0.2	0.2	0.4	0.8	0.1	0.9	0.1
Impala	0.3	0.4	0.1	0.8	0.1	0.9	0.4	0.4	0.3	0.4	0.2	0.6	0.6	0.5	0.6

E. rigidior (ERRI), Urochloa mosambicensis (URMO) and Panicum deustum (PADE). Selection also occurs for sites of high lateral cover (LCC), eg. thickets with relatively short to medium grass heights. This period, relative to the first two depicts a greater preference for areas comprising of both greater lateral cover and high ratios of palatable to intermediate grass species. Hence, in comparison to the previous two periods, the structural components play only a minor role in the white rhinos' habitat selection with grass species composition being important.

Although still selecting for sites of high lateral cover, the white rhinos during the late-dry season show a high preference for the taller grasslands again with high palatable to intermediate ratios. The unpalatable grass species such as Elyonuris argenteus (ELAR), Cymbopogon species and Bothriochloa insculpta (BOIN) were either avoided or at least played no major role in habitat selection during this period.

To conclude, the factors important in white rhino habitat selection differ seasonally, thus suggesting that habitat diversity is neccessary for the survival of these animals in the reserve. In addition, the herbivores are still at reasonably low densities and yet there are still marked seasonal differences in their habitat selection. This again indicates the dependence on habitat diversity or heterogeneity for survival.

The wildebeest during the dry-season selected for similar habitat factors as the white rhinoceros. However, a greater preference was shown for areas of higher lateral cover, higher herbaceous cover and taller grasslands. Differences occurred in their selection for the dominant grass species in that higher selection indices were shown for areas dominated by Cynodon dactylon (CYDA), Aristida congesta (ARCO), Eragrostis rigidior (ERRI), Hyparrhenia hirta (HYHI), Brachyaria serrata (BRSE) and Pogonarthria squarrosa (POSQ). Thus, wildebeest tend to select for the taller grasslands with a high herbaceous cover.

The hartebeest selected for tall grasslands of relatively low canopy and low lateral cover but with high herbaceous covers. Grass species characteristic of the relatively lower successional stages were preferred, eg. Aristida congesta (ARCO), Rhynchyletrum repens (RHRE), Themeda triandra (THTR), E. gummiflua (ERGU), Hyparrhenia hirta (HYHI), Brachyaria serrata (BRSE), Digitaria eriantha (DIER) and Pogonarthria squarrosa (POSQ). Thus the only important structural feature in determining the hartebeests' habitat selection was grass height.

The zebra depict interesting results in that either a high selection or complete avoidance for certain habitat factors occurred. They were highly selective for the open woodlands with grasses ranging from 10 to 15 cm in height. Sites of low canopy cover (CCA), low lateral cover (LCA) and low (HEA) to medium (HCB) herbaceous cover were also preferred. Sites dominated by grass species such as Rhynchyletrum repens (RHRE), Heteropogon contortus (HECO), Themeda triandra (THTR), unpalatable species (UNPA), Loudetia flavada (LOFL), Sporobolus pyrimedalis (SPPY) and Setaria nigrirostris (SENI) were highly preferred whereas, sites dominated by Cynodon dactylon (CYDA), E. curvula (ERCU), E. rigidior (ERRI), E. gummiflua (ERGU), Bothriochloa insculpta (BOIN), Urochloa mosambicensis (URMO), Digitaria eriantha (DIER), Panicum deustum (PADE), P. coloratum (PACO), Chloris virgata (CHVI) and Eragrostis. species (ERCR) were generally avoided. The areas selected by the zebra were characteristic of the hillside savannas which supported a relatively higher density of zebra during the dry season. Hence in this species habitat selection was based to a large extent on the structural components.

Impala selected for areas of relatively high canopy and lateral cover with short to medium grass heights typical of Acacia and riverine thickets. Grass species such as Bothriochloa insculpta (BOIN), Urochloa mosambicensis (URMO), Sporobolus pyramidalis (SPPY), Chloris virgata (CHVI) and Eragrostis species (ERCR) were highly selected with relatively complete avoidance for site factors typical of the more open habitats. Hence both the structural components and the grass species composition play an important role in the impalas' habitat selection

To conclude, Correspondence Analysis was able to extract and identify those habitat factors to which the herbivores either selected or avoided. However, this study was only able to analyze habitat selection based on the general habitat factors. The more subtle features, such as the effects of different nutritional values of the plant species, would have to be analyzed using experimental studies where comparisons can be made on both the feeding and non-feeding sites.

It is suggested from this analysis that certain physical characteristics of the habitat influences the habitat selection by the herbivores. The next section deals with dietary selection and its relationship to certain habitat factors.

4.4.3 Dietary Selection of the Five Main Grazers

4.4.3.1 Seasonality in the White Rhinos Diet

4.4.3.1.1 Overall Diet

The seasonal variation in the diet of the white rhinoceros is first considered and then related to the dietary selection of the other four grazers during the dry season.

Table 4.7 and Appendix F gives the results of the seasonal changes in the dietary preferences of the white rhinos, averaged for all habitat types. Only the grasses comprising over five percent of the diet or over five percent availability for at least one of the grazers are considered in the analyses. The seasons cover the months discussed in section 3.3.3.

Eighteen different grass species were recorded in the diet of the white rhinoceros population at Pilanesberg. However, only 6 of the species comprised about 70% of their diet with Eragrostis superba (average 10.3%), Heteropogon contortus (average 19.2%), Hyparrhenia hirta (average 12.5%), Panicum deustum (average 11.6%) and Urochloa mosambicensis (average 9.4%) being the most

Table 4.7.

Seasonal changes in the Percentage Contribution in the diet, of the grass species, for the white rhino at Pilanesberg. Standard errors are given in parentheses. A key to the grass species is given in Appendix F.

Species	Fire	Early wet	Late wet	Early dry	Late dry
CYDA	20.9(8.0)	0.8(1.5)	5.8(3.3)	2.3(1.8)	4.3(3.7)
RHRE	1.9(1.1)	4.4(1.4)	0.2(0.6)	4.5(2.5)	4.9(4.0)
HECO	21.2(5.1)	13.0(6.1)	11.3(4.9)	26.5(6.5)	24.1(9.3)
THTR	4.1(0.7)	0.7(1.3)	1.4(1.7)	6.6(3.1)	4.4(3.8)
ERCU	5.0(3.5)	4.2(3.4)	10.1(4.6)	4.3(2.5)	3.4(3.3)
ERSU	12.9(3.9)	23.8(8.4)	4.3(2.9)	2.3(1.8)	8.2(5.2)
ERRI	2.9(1.6)	1.6(2.1)	6.6(3.7)	4.1(2.4)	3.1(3.1)
ERGU	3.8(3.3)	0.0(0.0)	0.0(0.0)	0.0(0.0)	0.6(1.3)
HYHI	23.2(5.5)	19.0(7.4)	1.5(1.7)	3.7(2.3)	15.0(7.2)
BOIN	0.0(0.0)	0.0(0.0)	2.5(2.2)	0.7(1.0)	0.0(0.0)
BRSE	0.3(0.3)	6.2(4.1)	0.1(0.4)	6.8(3.1)	2.1(2.6)
URMO	1.7(1.4)	9.4(5.1)	27.4(7.8)	5.3(2.8)	3.1(3.1)
LOFL	0.0(0.0)	0.0(0.0)	0.0(0.0)	0.0(0.0)	0.0(0.0)
DIER	2.2(1.2)	3.4(3.0)	5.2(3.3)	5.4(2.8)	5.0(4.0)
PADE	0.0(0.0)	6.3(4.1)	18.8(6.4)	20.6(5.7)	12.5(6.5)
PACO	0.0(0.0)	0.0(0.0)	3.5(2.7)	5.6(2.8)	9.3(5.6)
SPPY	0.0(0.0)	7.3(4.5)	1.5(1.7)	1.2(1.2)	0.0(0.0)
UNPA	8.0(2.3)	15.0(6.5)	2.0(2.0)	1.0(1.2)	0.0(0.0)

important throughout the year. Similar results were found by Owen-Smith (1973) in the Umfolozi population with *Themeda triandra* (35.5%) being the most important grass species.

The main seasonal differences in the white rhinos diet concerns the significant increase or decrease in one or more of the following species (refer to Appendix); *Digitaria eriantha* (DE), *Cynodon dactylon* (CD), *E. superba* (ES), *E. rigidior* (ER), *Heteropogon contortus* (HC), *Hyparrhenia hirta* (HH), *E. curvula* (EC), *Brachyaria serrata* (BS), *Themeda triandra* (TT), *Panicum deustum* (PD), *P. coloratum* (PC), *Urochloa mosambicensis* (UM), *Sporobolus pyramidalis* (SP) and unpalatable species (UP).

Dietary selection during the fire and early-wet seasons both appear to be similar in terms of grass species selection, except for a significant decrease in the use of *Cynodon dactylon* ($t=7.77$, $p<0.001$) and increase in *Heteropogon contortus* ($t=3.24$, $p<0.001$). Thus the bulk of the white rhino's diet during these periods consisted of *Eragrostis superba* (ES), *Heteropogon contortus* (HC), *Hyparrhenia hirta* (HH) and to a lesser extent, *Cynodon dactylon* (CD) and unpalatable species (UP).

It is interesting to note that during the flush after a burn, and during the early-wet season, unpalatable grass species (UP) such as *Cymbopogon excavatus* and *Elyonurus argenteus* were present in their diet.

During the latter part of the wet season, the white rhinos showed an increase in selection for *Panicum deustum* (PD) and *Urochloa mosambicensis* (UM) and, to a lesser extent *Digitaria eriantha* (DE), *Cynodon dactylon* (CD), *E. rigidior* (ER), *Panicum coloratum* (PC) and *Bothriochloa insculpta* (BI). In contrast, the selection for *E. superba* ($t=7.40$, $p<0.001$), *Hyparrhenia hirta* ($t=7.38$, $p<0.001$), *Brachyaria serrata* ($t=4.64$, $p<0.001$), *Sporobolus pyrimedalis* ($t=3.23$, $p<0.01$) and unpalatable species ($t=5.65$, $p<0.001$) declined during the late wet season.

The early-dry season showed a similar dietary selection as the previous season with only significant differences in *Rhynchyletrum repens* (t=-4.96, p<0.001), *Heteropogon contortus* (t=-5.88, p<0.001), *Brachyaria serrata* (t=-7.21, p<0.001), *Themeda triandra* (t=-4.91, p<0.001) and which increase, and *Cynodon dactylon* (t=3.51, p<0.01), *Eragrostis curvula* (t=3.25, p<0.01) and *Urochloa mosambicensis* (t=8.14, p<0.001) which decrease. Both *Heteropogon contortus* (HC) and *Panicum deustum* (PD) account for just under 50% of their diet during this period.

Significant dietary changes occurred during the late-dry season in selection for *Eragrostis superba* (t=-3.52, p<0.01) and *Hyparrhenia hirta* (t=-4.78, p<0.001) which increase, and *Brachyaria serrata* (t=3.73, p<0.01) and *Panicum deustum* (t=2.74, p<0.01) which decrease. The white rhinos' diet during this period consists mainly of *Heteropogon contortus* (HC), *Hyparrhenia hirta* (HH), *Panicum deustum* (PD) and *P. coloratum* (PC) totalling to approximately 51%.

To summarize, high selection for palatable species such as *Eragrostis superba* (ES), *Heteropogon contortus* (HC), *Hyparrhenia hirta* (HH), *Panicum deustum* (PD), *P. coloratum* and *Urochloa mosambicensis* (UM) was evident and together accounted for over 60% of their annual diet. Significant changes occur between one or more of the above grass species depending on the season and the habitat (see below). Minor changes occurred between the less dominant species such as *Cynodon dactylon* (CD), *Rhynchyletrum repens* (RR), *Eragrostis rigidior* (ER), *E. curvula* (EC), *Brachyaria serrata* (BS), *Themeda triandra* (TT) and *Panicum coloratum* (PC).

4.4.3.1.2 Relationship between Diet and Habitat Choice

Appendix G shows the seasonal differences in the percentage contribution to the diet (PC), and the preference indices (PI) for the grasses eaten by the white rhinos within each habitat type. It is evident that diet changes not only seasonally but also within each habitat type. However because of the small sample size per habitat, the grass species were categorized as either palatable-tall, palatable-creeper, intermediate or unpalatable (see Table 3.). The percentage contribution of each dietary type is given in Table 4.8

During the fire period, valley savannas and secondary grasslands were mainly selected (see Figure 4.1), hence dietary differences only within these two habitats were considered. In both habitats the palatable species such as *E. superba* (ES) and *Heteropogon contortus* (HC), the intermediate species such as *Themeda triandra* (TT), *Eragrostis curvula* (EC), *E. rigidior* (ER), *Hyparrhenia hirta* (HH) and *Digitaria eriantha* (DE), and unpalatable species (UP) were preferred.

Similarities in the overall feeding patterns in both habitat types is confirmed by the Chi-square test results. However there was a slight preference for the two palatable feeding categories in the secondary grasslands. There was no significant difference in the selection for the various dietary types in the valley savannas, thus indicating that no preference for the particular grass species occurred during this period. A similar phenomenon of no preference for dietary types also occured during the early-wet season, and may be attributed to the fact that most grass species tend to be highly nutritious during the rainy season.

The late-wet season showed a tendency for the white rhinos to select *Acacia* and riverine thickets, valley savannas and termitaria to a greater extent than during the previous two seasons. There was no significant difference in the white rhinos' feeding pattern between the valley savannas and termitaria, except avoidance for the unpalatable species was apparent in the valley savannas. However, significant differences did result between the intermediate and the two palatable feeding types in the termitaria. Despite this, significant differences were shown in their diets between the habitats, with a high preference for *Heteropogon contortus* ($t=6.20$, $p<0.001$), *E. superba* ($t=3.51$, $p<0.001$), and *Sporobolus pyrimedalis* ($t=4.03$, $p<0.001$) in the valley savannas, and *Urochloa mosambicensis* ($t=3.11$, $p<0.001$), *Digitaria eriantha* ($t=4.09$, $p<0.001$) *P. deustum* ($t=7.79$, $p<0.001$)

and *P. coloratum* ($t=5.16$, $p<0.001$) in the termitaria sites.

During the early-dry season again no significant difference was apparent in the white rhinos' feeding pattern between the two habitat types. In the valley savannas the palatable-tall species such as *Heteropogon contortus* (average 34.3%), *Themeda triandra* (average 14,3%), *Digitaria eriantha* (average 8.7%) and *Hyparrhenia hirta* (average 7.1%) were highly preferred. The rhinos also showed an increase in the selection for the palatable-tall species such as *Heteropogon contortus*, *Brachyaria serrata*, *Digitaria eriantha*, *Panicum deustum* and *P. deustum* in the secondary grasslands, termitaria or *Cynodon dactylon* patches and thickets.

It is interesting to note that, although the white rhinos showed a high preference for the *Cynodon dactylon* "lawns" (approximately 2% of the available grassland), this particular grass species was generally avoided.

Their dietary selection during the late-dry season was similar to the early-wet season and the fire period with a high preference for the palatable-tall species such as *Heteropogon contortus* (HC), and *Digitaria eriantha* (DE). However, there was an increase in the selection for both *P. deustum* (PD) and *P. coloratum* (PC) during this season as opposed to the fire and early-wet periods. In both habitats the unpalatable species were avoided while the palatable-creeper species were only slightly selected.

Thus, although the white rhinos utilized a wide range of grass species, only a third of them were highly selected throughout the year (Appendix G). During the fire period, however, most of the species represented in their diets did not differ greatly from their availability in the grasslands. The white rhinos generally selected for the palatable-tall and intermediate grass species.

Unpalatable species, such as *Cymbopogon excavatus*, *Elyonurus argenteus* and *Bothriochloa insculpta*, were generally avoided. However they were grazed when short (eg. during the fire and early-wet periods) and occasionally during the early-dry season when tall stands of *Bothriochloa* were utilized.

Owen-Smith (1973) observed that the white rhino food selection at the Umfolozi Game Reserve was based largely on grassland type, ie. dominant species, rather than individual species. This tends to agree with the observations and analyses discussed in the previous sections on the Pilanesberg rhinos. The white rhinos at Pilanesberg showed a high preference for certain grass types (eg. palatable-tall and intermediate) irrespective of their availability. In addition, the Correspondence Analysis was able to show that both the grassland structure and grass species composition influenced herbivore feeding selection. There was also a tendency for the white rhinos to show a seasonal selection for grasslands of various heights. For example, during the fire period and most of the wet season, white rhinos concentrated their grazing on the shorter grasslands generally feeding randomly on most grass species. Most of the grasslands selected, eg. secondary grasslands, valley savannas and *Cynodon* "lawns", were under 15 cm tall.

As conditions became drier increasing use was made of the taller grasslands with a greater preference shown for the more palatable tall species such as *Heteropogon contortus*, *Eragrostis superba*, *Panicum maximum* and *P. coloratum*. This supports the results collected by Melton (1978), who showed that the white rhinos fed mainly on *P. maximum* and *Themeda triandra* during both seasons, although a greater variety of grass species was consumed during the drier months.

Initially the animals concentrated on the localized short patches, particularly those around termitaria, but as progressive drying and food depletion occured a switch was made to the taller grasslands greater than 15 cm in height. The short grasslands provide food only during the growing season. To carry them through the dry season, the white rhinos are dependent on the remaining taller grasslands. The availability of this sub-maintenance forage during the drier months therefore becomes critical.

Owen-Smith (1973) showed a similar trend with the white rhinos moving into the margins of the tall Themeda triandra stands thus expanding the extent of the short grass areas. He was able to demonstrate a seasonal movement along a catena with the animals progressively moving up as the seasons became drier. A similar situation was not found at Pilanesberg possibly for two reasons;

(i) most of the slopes are too steep and therefore inaccessible to the white rhino, and
(ii) the rhino population at Pilanesberg is at a relatively lower density than at the Umfolozi Game Reserve (0.005 animals per ha as opposed to over 3 per ha).

4.4.3.2 **Dietary Selection by the Other Large Grazers**

Dietary selection by the four other large grazers was only recorded during the dry season for two reasons. Firstly, because of the time restriction, greater emphasis was placed on the white rhinoceros; and secondly, because this period is believed to be most critical for grazing herbivores in terms of food limitation. Thus dietary selection and their degree of overlap would be the most important during this period.

Table 4.8 and Appendix H give the grass species composition in the diet of the other four large grazers for the early-dry and late-dry seasons. These results have been averaged for all the vegetation types. Appendix H gives the percentage contribution in the diet (PC) and the Preference Indices (PI) of the grasses consumed in each habitat type.

4.4.3.2.1 **Hartebeest**

Table 4.8 shows the dietary selection by hartebeest for the two parts of the dry season. Grass species such as Rhyncheletrum repens, Hyparrhenia hirta, Heteropogon contortus and Themeda triandra were highly selected during both seasons, although

Table 4.8 : Percentage Contribution in the diet (PC) and Preference Indices (PI) for grasses eaten by the other large herbivores, by habitat and season. A key to the grass species is given in Table 4.1

		CYDA		RHRE		HECO		THTR		ERCU		ERSU		ERRI		ERGU		HYHI		BOIN	
SEASON	HABITAT	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI
Hartebeest (early dry)	SECGLD	0.0	0.0	31.1	3.3	13.1	0.9	8.4	2.3	1.0	0.2	5.4	0.6	3.7	0.6	3.4	4.9	8.2	1.0	0.0	0.0
Hartebeest (late dry)	SECGLD	0.1	0.1	38.7	4.1	0.0	0.0	6.7	1.8	0.0	0.0	9.3	1.0	3.1	0.5	7.2	10.3	16.5	2.1	0.0	0.0
	VALSAV	1.4	0.2	0.1	0.1	22.1	1.4	11.2	2.3	4.7	2.0	1.4	0.6	0.1	0.1	12.0	30.0	0.0	0.0	0.0	0.0
Wildebeest (early dry)	SECGLD	0.1	0.1	24.0	2.5	28.5	1.9	0.0	0.0	7.8	1.9	8.2	0.9	10.4	1.8	0.0	0.0	0.1	0.1	0.0	0.0
	VALSAV	0.0	0.0	0.0	0.0	78.0	5.0	0.0	0.0	5.0	2.1	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.2	0.0	0.0
	PEDGLD	0.0	0.0	0.0	0.0	10.0	0.7	0.0	0.0	4.0	3.6	20.0	15.4	19.0	11.9	1.0	0.2	0.0	0.0	0.0	0.0
Wildebeest (late dry)	SECGLD	3.3	0.3	38.5	4.1	4.8	0.3	10.6	2.9	0.1	0.1	0.1	0.1	6.4	1.1	0.0	0.0	0.0	0.0	0.0	0.0
	VALSAV	3.0	0.5	1.7	0.5	0.1	0.1	4.5	0.9	7.0	2.9	0.1	0.1	1.7	0.8	1.7	4.3	12.3	2.5	0.6	0.8
	PEDGLD	0.1	0.1	2.0	0.5	14.4	1.0	10.9	10.9	0.1	0.1	14.4	11.1	0.0	0.0	0.0	0.0	14.9	0.8	0.0	0.0
Zebra (early dry)	SECGLD	0.0	0.0	0.0	0.0	28.1	1.9	24.5	6.6	0.0	0.0	1.0	0.1	0.0	0.0	1.5	2.1	10.7	2.7	0.0	0.0
	VALSAV	0.0	0.0	0.1	0.1	30.5	1.9	2.4	0.5	0.0	0.0	32.9	3.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Zebra (late dry)	HILSAV	0.0	0.0	0.1	0.1	52.9	1.3	9.1	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Impala (dry)	VALSAV	22.0	1.7	0.0	0.0	1.0	0.1	0.0	0.0	10.0	4.2	0.0	0.0	4.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0
	THICKET	6.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	5.0	1.1	0.0	0.0	1.0	0.5	0.0	0.0	4.0	1.2	0.0	0.0

(PAL, INT and UNP are the proportions of palatable, intermediate and unpalatable grass species, respectively).

SECGLD = Secondary grasslands
PEDGLD = Pediment grasslands
VALSAV = Valley savannas
HILSAV = Hillside savannas
THICKET = *Acacia* and riverine thickets

Table 4.8 : (Cont.)

SEASON	HABITAT	BRSE		URMO		LOFL		DIER		PADE		PACO		SPPY		UNPA					
		PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PAL	INT	UNP	n
Hartebeest (early dry)	SECGLD	15.5	14.1	2.5	0.5	0.0	0.0	2.8	1.1	0.0	0.0	1.0	1.0	0.0	0.0	0.1	0.1	45.9	54.0	0.1	9
Hartebeest (late dry)	SECGLD	0.0	0.0	3.6	0.7	0.0	0.0	8.2	3.3	0.0	0.0	6.2	6.2	0.0	0.0	0.0	0.0	25.8	74.2	0.0	4
	VALSAV	0.0	0.0	5.4	3.2	2.9	2.6	22.5	14.1	0.0	0.0	9.4	3.8	2.9	7.3	0.0	0.0	49.5	50.5	0.0	5
Wildebeest (early dry)	SECGLD	2.8	2.5	5.6	1.1	0.0	0.0	11.3	4.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	45.1	54.9	0.0	5
	VALSAV	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15.0	16.7	0.0	0.0	1.0	2.5	0.0	0.0	93.0	7.0	0.0	3
	PEDGLD	28.0	20.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	19.0	19.0	0.0	0.0	0.0	0.0	77.0	23.0	0.0	3
Wildebeest (late dry)	SECGLD	0.0	0.0	14.8	3.0	0.0	0.0	3.3	1.3	12.7	12.7	4.5	4.5	0.0	0.0	0.0	0.0	47.5	52.5	0.0	6
	VALSAV	0.0	0.0	4.9	2.9	0.0	0.0	6.0	3.8	0.0	0.0	0.0	0.0	5.3	13.3	0.0	0.0	9.6	90.4	0.0	6
	PEDGLD	27.4	19.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	14.4	14.4	0.0	0.0	0.0	0.0	81.5	18.5	0.0	3
Zebra (early dry)	SECGLD	33.7	30.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	87.4	12.6	0.0	5
	VALSAV	5.4	6.0	0.0	0.0	13.2	12.0	3.8	8.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	71.2	28.8	0.0	5
Zebra (late dry)	HILSAV	12.3	1.2	0.0	0.0	9.8	1.0	6.4	6.4	0.0	0.0	0.0	0.0	8.3	0.5	0.0	0.0	74.3	25.7	0.0	6
Impala (dry)	VALSAV	0.0	0.0	2.0	0.2	0.0	0.0	22.0	13.8	22.0	9.0	0.0	0.0	0.0	0.0	0.0	0.0	25.0	75.0	0.0	2
	THICKET	0.0	0.0	3.0	0.3	0.0	0.0	0.0	0.0	68.0	9.3	0.0	0.0	16.0	7.3	0.0	0.0	71.0	29.0	0.0	2

Eragrostis gummiflua (t=-2.12, p<0.01) and *Digitaria eriantha* (t=-3.61, p<0.01) significantly increased while *Rhyncheletrum repens* decreased (t=3.88, p<0.01).

Section 3.3.3.2 examined the habitat selection of the hartebeest, depicting a high preference for secondary grasslands with intermittent selection for valley savannas. Hence, dietary differences only occurred between these two habitats.

Palatable species such as *Themeda triandra* (TT), *Digitaria eriantha* (DE), and *Panicum coloratum* (PC) were highly selected in both habitats. The intermediate grass species, *Rhyncheletrum repens* (RR), contributed over 30% of their diet in the secondary grasslands, whereas the palatable species such as *Themeda triandra* (TT), *Heteropogon contortus* (HC), and *Digitaria eriantha* (DE) contributed over 50% in the valley savannas.

Although showing distinct habitat differences in their diet, the hartebeest tended to select for the more palatable to intermediate grass species (see Table 4.8).

4.4.3.2.2 Wildebeest

The wildebeests' diet was similar to that of the hartebeest, except more time was spent foraging on grass species found in the valley savannas. Very little seasonal differences (early-dry and late-dry) in their diet could be detected (see Appendix H), except that *Heteropogon contortus* (HC) showed a marked decrease during the latter part of the dry season (t=6.78, p<0.001).

Both *Rhynchyletrum repens* (RR) and *Heteropogon contortus* (HC) accounted for over 40% of the wildebeests' diet in the secondary grasslands. During the early part of the dry season palatable species such as *Heteropogon contortus* (HC) and *P. deustum* (PD) were highly selected, whereas the intermediate species *Hyparrhenia hirta* (HH) and to a lesser extent *Eragrostis curvula* (EC) were important during the late-dry season. In the pediment grasslands palatable species such as *Heteropogon contortus* (HC), *Brachyaria serrata* (BS) and *Panicum coloratum* (PC), and the intermediate species *Eragrostis superba* were selected during this season.

Hence, the palatable-tall species, *Rhynchetrum repens* (RR), *Heteropogon contortus* (HC) and, to a lesser extent *Themeda triandra* (TT), *Brachyaria serrata* (BS) and *Digitaria eriantha* (DE), and the intermediate species, *Rhyncheletrum repens* form the bulk of their winter diet. Thus more palatable species were favoured in all the vegetation types. Similar results were obtained by Melton (1978) who showed that the wildebeest in the Umfolozi Game Reserve selected mainly for *Digitaria macroglossa*, *Heteropogon contortus*, *Eragrostis superba*, *Themeda triandra*, *Panicum coloratum* and *Sporobolis smutsii* during the winter months.

4.4.3.2.3 Zebra

The zebra, with their tendency to select secondary grasslands and valley savannas during the early-dry season and hillside (mainly mesocline) savannas during the late-dry season, showed preferences for grasses common in these habitats. For instance, palatable-tall species such as *Heteropogon contortus* (HC), *Themeda triandra* (TT) and *Brachyaria serrata* (BS), and the intermediate species *Hyparrhenia hirta* (HH), were favoured in the secondary grasslands, and *Heteropogon contortus* (HECO), *Eragrostis superba* (ERSU) and *Loudetia flavada* (LOFL) in the valley savannas. During the late-dry season *Heteropogon contortus* (HECO), *Themeda triandra* (THTR), *Brachyaria serrata* (BRSE), *Loudetia flavada* (LOFL), *Digitaria eriantha* (DIER) and *Sporobolus pyramidalis* (SPPY) contributed over 80% of their diet in the hillside savannas. By referring to Table 3.1 it is apparent that the grass species selected in this habitat are those most readily available. Hence, a high preference was made for the palatable-tall grass species especially in the secondary grasslands ($t=2.92$, $p<0.001$). The selection for the tall species confirms the results obtained in the Correspondance Analysis which depicted a close relationship between the zebra and tall grasslands.

The grass species, *Heteropogon contortus* ($t=-6.04$, $p<0.001$), *Themeda triandra* ($t=5.66$, $p<0.001$), *Brachyaria serreta* ($t=-4.34$, $p<0.001$), *Loudetia flavada* ($t=-6.89$, $p<0.001$), and *Sporobolus pyramidalis* ($t=-9.38$, $p<0.001$) significantly increased, while, *Eragrostis superba* ($t=5.31$, $p<0.001$) and *Digitaria eriantha* ($t=4.68$, $p<0.001$) significantly decreased from one season to the next.

Melton (1978) found that the Umfolozi zebra mainly utilized palatable species such as *Panicum maximum*, *Themeda triandra* and *Heteropogon contortus*. The zebra in the Pilanesberg Game Reserve showed similar preferences in that the palatable species contributed to over 70% of their dry season diet.

4.4.3.2.4 Impala

Unfortunately, only four feeding sites were recorded for this species during the dry season, two in the valley savannas and two in the *Acacia* and riverine thickets. These were however, able to give some indication as to what grass species were preferred.

The palatable-tall species, *Panicum deustum* was highly preferred (PI of over 9.0) in both habitat types and contributed to about 50% of their diet. Palatable species such as *Digitaria eriantha* (DE) and *Cynodon dactylon* (CD), and the intermediate species *Eragrostis curvula* (EC) were utilized to a greater extent in the valley savannas.

Impala were observed to utilize only the highly palatable grass species during the dry season, especially in the thickets. Similar results were obtained by Melton (1978), who showed that the impala in the Umfolozi Game Reserve preferred mainly *Panicum maximum* in both the wet and dry seasons.

CHAPTER FIVE

HABITAT AND DIETARY OVERLAP BETWEEN THE PILANESBURG GRAZERS:

5.1 Introduction:-

The major focus in studies of community structure is the use of pattern of resource partitioning as a basis for explaining the coexistence of ecologically similar species (eg. Pulliam and Parker, 1979). Essentially ecological community theory attempts to predict the numbers and relative abundance of coexisting consumer species based on the availability of resources, and the resource utilization patterns of the species (MacArthur and Levins, 1967; MacArthur and Wilson, 1967; Levins, 1968; MacArthur, 1972; May, 1973; Pulliam, 1983). The procedure requires the calculation of firstly, carrying capacities for each species based on the availability of resources and secondly, competition coefficients for each species pair, based on the similarity of their resource utilization patterns (Pulliam, 1983).

Although the precise application and interpretation of ecological niche overlap remain a subject of debate, many ecologists nevertheless use various overlap measures to indicate degrees of ecological similarity within assemblages of species. Studies by Pianka (1975) and Cody (1974) made extensive use of niche overlap data when studying interspecific competition. Hurlbert (1978) suggested that niche overlap measures should serve "as a foundation for discussion of resource utilization strategies, competition, species packing, and so on".

The term niche has been variously defined by many authors. Elton (1927) considered the niche as the fundamental role of an organism in a community - what it does, its relationship to its food and to its enemies. Grinnell (1924) on the other hand, referred to the niche as a subdivision of the environment occupied by a species. Hutchinson (1959) conceptualized the niche as a combination of the functional role of an organism in an ecosystem as well as its position in time and space. He therefore defined the niche of a species as an "n-dimensional hypervolume". Levins (1968) went further by stating that "niche dimensionality refers not to the number of biologically relevant factors in the environment, but to the number of factors which serve to separate species". Thus before attempting any niche study, it is important to know the species concerned and to identify those environmental factors to which they respond. Separate divisions or dimensions of the various resource types utilized by the species can then be defined. Each resource dimension is then treated as a single niche in an Euclidian space of many dimensions (Slobodchikoff and Schulz, 1980). It should be noted that these dimensions are not gradients of a resource, as is often implied (ref), but consist of discrete resource entities. For example, a herbivores diet cannot be interpreted as a gradient of grass species but rather a resource dimension consisting of a number of resource types.

Few studies on the interspecific interactions within entire large herbivore communities have been attempted in Africa (eg. Versey-Fitzgerald, 1960, 1965; Lamprey, 1960; Field, 1968; Bell, 1969; Field and Laws, 1970; Ferrar, 1973; Ferrar and Walker, 1974; Page and Walker, 1978; Attwell, 1978). Thus, the aim of this section is to analyze the nature and the relative importance of those factors which serve to separate the species, eg. white rhinos and their potential competitors in a southern African game reserve.

5.1.1 Relationships Between Overlap, Similarity, and Competition:

Before examining the various methods of estimating niche overlap, a clear understanding of the relationships and differences between the overlap, similarity and competition coefficients, as explained by Lawlor (1980), are neccessary.

Overlap measures are designed to measure the degree to which two species share a set of common resources or utilize the same parts of the environment (Lawlor, 1980). In other words, it is the region of niche space (in the sense of Hutchinson, 1958) shared by two or more contiguous niches (Colwell and Futuyma, 1971). These overlap measures are usually scaled from zero to one; zero indicating no overlap, and one indicating complete overlap. Resource use can be expressed as Pik, the proportion of consumer species' (i) total utilization that is represented by each resource, k. The proportion of food type (j) depends on two factors; the consumer's electivity, and the availability of that food type in the environment. Schoener (1974) defined electivity as the consumer's relative ability (or preference) to catch and consume an item of a particular food type. If all resource types are equally abundant then their relative proportions in the diet are determined only by their relative electivities. Lechovicz (1982) referred to the electivity indices as measures of the utilization of food type (r) in relation to their abundance or availability (p) in the environment. Therefore, foods that constitute a larger proportion of the diet than of the available foods are considered to be preferred. If a particular food type is relatively scarce it may represent only a small proportion of the consumer's diet, even though the consumer has a high electivity for that food type (Lawlor, 1980).

Measures of similarity are often used in comparisons between closely related species living in different communities or environments. However, the problem with this measure is that the resources may differ in abundance between the environments thus creating two major problems. Firstly, similar species may not appear alike if living in totally different environments, and secondly, the converse situation may arise where species which are very dissimilar may appear quite similar because of the species - environment interactions (Lawlor, 1980). Consequently, conclusions about species' similarities based on their overlaps may be misleading. It is therefore important to be quite sure whether one is interested in comparing the species themselves or the species-environment relationships. Lawlor (1980), when considering consumer similarities, concluded that they should be based on patterns of resource use rather than patterns of the resources used. Thus, the use of electivities rather than proportional utilizations should be used in any measure of similarity. This ensures that species with similar electivity patterns will appear similar even if compared in different environments with different resource abundances. Lawlor (1980) modified the Symmetric MacArthur-Levins formula (discussed later) to measure species similarities based on consumer electivities;

$$Sij = \frac{\sum(aik \times ajk)}{\sum(aik)^2 \times \sum(ajk)^2} \quad ......5.1$$

where a is the electivity of resource k by species i and j, and S is the similarity index.

The main emphasis of this chapter and the next is to incorporate competition indices, using overlap measures, to calculate stocking densities, whether at carrying capacity or at a particular maintained level of utilization. The theory of competition implies that the greater the overlap in resource use between two organisms, the greater the competition coefficient, and hence the greater the intensity of competition. By definition, competition occurs when two or more organisms interfere with or inhibit one another (Pianka, 1981). Competition can be quite direct as in the case of interspecific territoriality (eg. Brown, 1964), and is then termed "Interference Competition" (Elton and Miller, 1954; Miller, 1967). More indirect competition may also occur, such as that arising through the joint use of the same limited resources, this being termed "Exploitation Competition" (Elton and Miller, 1954; Miller, 1967). In this case, although the resource pool is reduced in availability to the competing individuals, no direct interactions are apparent (MacNaughton and Wolf, 1973).

As mentioned earlier,the degree of resource overlap has often been used as a measure of the intensity of interspecific competition (eg. Schoener, 1968; Levins, 1968; Cody 1974, Culver 1974, Pianka 1973, 1975; May, 1975) whereby a positive relationship has been assumed between the two measures. Pianka (1972, 1974) on the otherhand, postulated an inverse relationship between the intensity of competition and the degree of niche overlap (termed the "Niche Overlap Hypothesis"). He reasoned that if resources are not in short supply, "extensive niche overlap may actually be correlated with reduced competition". "Disjunct niches on the otherhand may often indicate avoidance of competition where it could have been potentially severe". However, equating the degree of overlap to the intensity of competition can be dubious and misleading (Colwell and Futuyma, 1971). Mere overlap in resource use is no guarantee that competition is taking place. This is largely because:

(i) the resource may not be limiting and overlap therefore does not result in competition,

(ii) competition may be a complex function of overlap, and

(iii) low current overlap may be the result of past competition (Colwell and Futuyma 1971, Hurlbert 1978, Petriatis 1975, Abrams 1980, Lawlor 1980, Slobodchikoff and Schultz 1980).

Hence the theory of niche overlap and competition can only be applied to systems which have limiting resources, eg. systems at, or close to carrying capacity. If one wishes to maintain a system at a level of utilization well below carrying capacity then competition is negligable - resources are not limiting hence, negligible interspecific interactions. However, if the objectives of a reserve is to allow the density of one of the species to increase while maintaining a specified level of utilization, then the species' overlap coefficients become important. Those species which depict high overlap with this species will most likely be the ones which modify the grazing level. For example, by increasing species A, species B, which has similar requirements, must be reduced otherwise the overall grazing pressure will exceed the specified level.

Rosenzweig (1974, 1979, 1981) and Pimm and Rosenzweig (1981) have presented an interesting model with regards to habitat selection and competition. They propose that sympatric species, foraging optimally, avoid competition by utilizing different habitats, ie. differential habitat selection reduces competition, sometimes to zero. The important point arising from this model is that although competitive interactions do not have to prevail at every possible density pair, they do have to produce an overall depression of the densities. Consequently, relating niche overlap to the degree of competition becomes meaningless, because at the stable node competition will be zero. However, Rosenzweig (1981) argued that instead of trying to relate competition to niche overlap one should rather discover whether the position of the species' equilibriums are below their carrying capacities.

The major critism of his model is that it depends entirely on the theory of optimal foraging (Schoener, 1974; Pyke, et al, 1977), of which to date few convincing studies are available. Nevertheless, a number of important implications can be extracted from their model. They are:

(i) there are thresholds at which one species will outcompete another.

(ii) when at moderate densities, the increase of one species may not cause the decrease of another.

Although it seems likely that zero competition at equilibrium may exist when one or more of the resources are limiting, its importance in structuring communities seems doubtful. Rosenzweig (1979, 1981) believes, as do many others (e.g. MacArthur and Levins, 1967; MacArthur and Wilson, 1967; Levins, 1968; May, 1973; Cody, 1974; Pianka, 1975; Pulliam, 1983), that competition itself gives rise to community equilibria. In other words, competition modifies the habitat requirements or preferences of the species, ie. competition behaves as a directive force in structuring ecosystems. They believe that continual adaptations of the components within an ecosystem occur as a result of their response to interspecific competition. An alternative explanation is proposed whereby a species' habitat selections are determined independently of each other during speciation, and thus overlap results incidentally to their past evolutionary history. Communities would therefore consist, to a large extent, of randomly assembled species. This has apparently been explained using models which randomly structure a known species assemblage and then test for significant differences between the randomly structured and the natural communities (eg. Sale 1974, Tompson and Rusterholz, 1982). If the random models are essentially similar to real communities, then one has to favour the theory that community structure is built up of a random accretion of components adapted in allopatry (ref).

Finally, it should be stresssed that when concerned with estimating stocking densities or carrying capacities in multispecies systems, the processes which structured the communities in the past, eg. competition and predation, are not as important as the ecological similarities or differences presently taking place. Interest was therefore placed only on the present interactions, or the contempory niche patterns, and not whether competition played an important role in structuring communities in the evolutionary sense. In addition, most communities, especially nature reserves, are comprised of a number of introduced and possibly alien species which have been translocated into areas which they would naturally not occur hence, unnatural processes were used to structure the community.

Thus this study was developed not to test whether competition is presently occurring between the Pilanesberg grazers, but rather to relate niche theory in estimating stocking densities in a multispecies system.

5.2 Methods:-

5.2.1 Field Data Collection:

In order to fulfil the objectives of this study it was necessary to systematically search for, and then measure and record the characteristic site attributes of each grassland site selected by the foraging herbivores. From these sites, information on both the habitat structure and dietary selection should be collected (see chapter 4).

Based on previous investigations (eg. Ferrar, 1973; Ferrar and Walker, 1974; Page and Walker, 1978; Attwell, 1978; Melton, 1978) and preliminary observations, the following dimensions were found to be important in describing the feeding niches of the five large grazers in the reserve;

(i) Habitat type, eg. whether in Secondary Grasslands, Pediment Grasslands, Valley Savannas, Mesocline Savannas, or Thickets.

(ii) Dietary component, ie. grass species.

The feeding niches of the herbivores can now be described along two dimensions in terms of Hutchinson's multidimensional hyperspace (Hutchinson, 1957). A third component, the subdivisions of the herbaceous component within the major habitat types, was analyzed using a multivariate technique known as Discriminant Function Analysis. This technique essentially reduces the multidimensional herbaceous component to a few dimensions. Overlap along the habitat niche dimension could be measured in more detail.

5.2.2 Calculation of Niche Overlap

5.2.2.1 Single Dimensions

Overlap has been quantified in numerous ways (MacArthur and Levins, 1967; Schoener, 1968; Colwell and Futuyma, 1971; Pianka, 1973;). The particular overlap index used is somewhat arbitrary, since similar qualitative results are obtained with a wide array of indices. Little or no explanation is given in the literature as to why a particular overlap index was used or not. An attempt is therefore made to examine the various methods in detail, emphasising their pros and cons.

The two most widely used methods are the Symmetrical and the Asymmetrical methods. The Symmetrical method was first presented by Pianka (1973). The equation produces a symmetrical matrix of α's so that

$$\alpha ij = \alpha ji$$

ie, the effect of species j on species i is equivalent to the effect of species i on species j and takes the form:

$$\alpha ij = \frac{\sum (Pik \times Pjk)}{\sqrt{(\sum Pik^2)(\sum Pjk^2)}} \quad ....5.2$$

Slobodchikoff and Schulz (1980) have pointed out three advantages of this method: (1) a ready geometrical interpretation, (2) the symmetrical nature of the matrix, and (3) the fact that alpha cannot exceed one.

The Asymmetrical method as proposed by Levins (1968) and MacArthur (1972) differs in that the overlap is expressed relative to only one of the species as follows:

$$\alpha ij = \frac{\sum (Pik \times Pjk)}{\sum (Pik)^2} \quad .....5.3$$

ie. it measures how much a species' utilization curve overlaps that of another species curve.

According to May (1975), the alpha matrix produced by this equation is not symmetrical, ie; αij will generally not equal αji. This is because Pik, the denominator, is a property of only the ith species (refer to Slobodchikoff and Schulz, 1980). In other words, pairwise overlap (αij) is calculated only with respect to species i. Values greater than one may now result depending on whether species j utilizes resource type k to a greater extent than species i, i.e. Pik is greater than Pjk. Its major disadvantage is that one must be extremely careful to count either all individuals of species i and j, or to count the same proportion of each species (Slobodchikoff and Schulz, 1980). For example, if species j is more successful at eluding the investigator than species i, it will skew the overlap value (αij), indicating, that less competitive pressure from j is being exerted on i than it really is. However, the Asymmetrical method remains the most popular for calculating niche overlap. This is mainly because it does not assume that both species have equal effects on each other and also, because it is closely related to the competition coefficient of the Lotka - Volterra formulation of interspecific competition (MacArthur, 1968; 1972; Schoener, 1974).

The overlap measures are best explained graphically using figure 5.1. If one considers a simple system of two species, one a specialist and one a generalist, foraging along a resource gradient, then the following becomes apparent. When using Pianka's Symmetrical method, overlap is calculated irrespective of the proportional resource use of each species. In other words, one is interested only in the extent to which both share common resources, ie, the degree of similarity (represented by A in Figure 5.1).

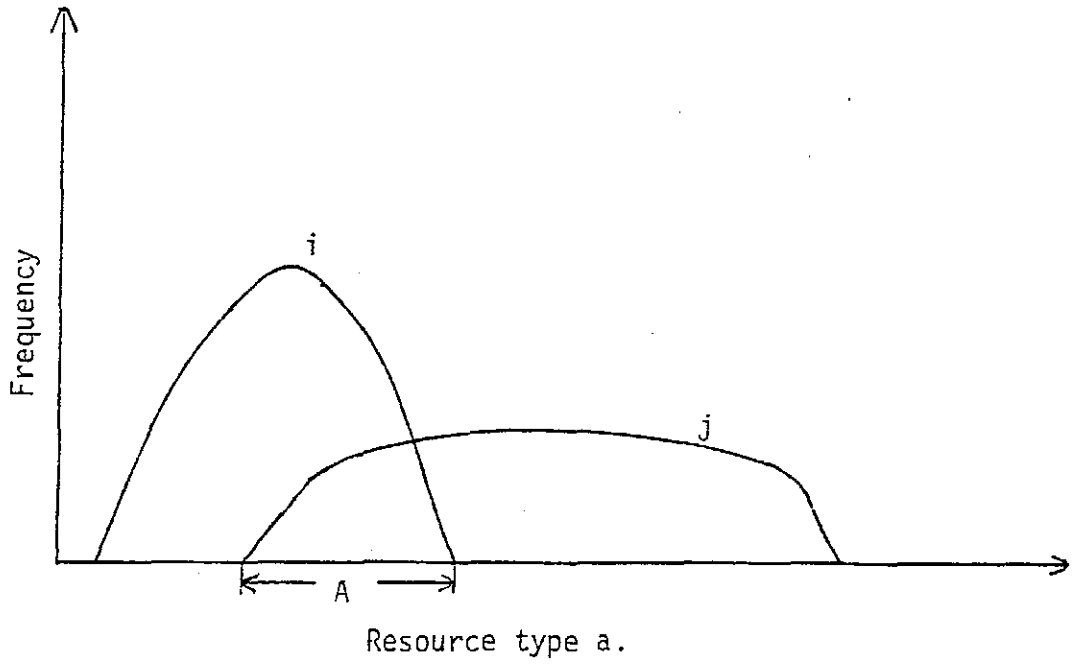


Figure 5.1 : Frequency distributions of two species, i and j, for the utilization of resource type a.

If interested in the niche overlap with respect to only one species, or the influence of one species on another, then the Asymmetrical method should be chosen. The measure therefore has two different values depending on whether one considers the effect of species j on species i, or vice versa. In the first instance, αji would be close to or greater than 1, whereas in the latter case αji would be less than 1.

Species i, being more specialized in its feeding requirements, shares only a small proportion of species j's total resource utilization. Species j, on the otherhand, is more of a generalist feeder, and consequently, shares a large proportion of species i's total resources. (The resource utilization strategies used here are those defined by Schoener, 1977; MacArthur, 1972 and Maynard Smith, 1974). When considering only those food types which are represented as A, in Figure 5.1, then species i utilizes them to a much greater extent than species j. Therefore, αji (overlap with respect to species i, the specialist) has a much greater value than αij (overlap with respect to species j, the generalist). This therefore explains why the two overlap values differ. If for example, the two species forage on a broad range of food types then the two values will differ only slightly. This occurs because both Pik and Pjk have similar values. The use of this method is best illustrated by referring to the following hypothetical example. The proportional use of four resources by two species is shown below;

Species	I	II	III	IV
1	0.6	0.4	0.0	0.0
2	0.2	0.3	0.4	0.1

Species 1 being more a specialist feeder consequently, utilizes resources I and II to a greater extent than species 2. This is revealed in the overlap measures using the Asymmetrical method, $\alpha 21 = 0.80$ and $\alpha 12 = 0.46$. Species 1, because of its greater use of resources I and II, exert a greater impact on species 2, than vice versa. Pianka's method, on the otherhand, predicts a single (mutual) overlap of 0.62.

The Asymmetrical method was therefore preferred to Pianka's method, and was subsequently used to determine the relative overlaps, along each dimension (habitat and diet) between the white rhinos and their associated grazers.

5.2.2.2 Multidimensional Overlap

Once the decision on which measure to use for estimating overlap along single resource gradients (e.g. diet or habitat) has been made, the next problem lies in assessing the combined effects of niche overlap along more than one dimension. Cody (1974) and May (1975) have both pointed out that either the Product (calculates the product of the overlap measures) or the Summation (calculates the mean of the overlap measures) methods may be used, depending on whether the resources or dimensions are dependent or independent. The Product method is generally used when resources are independent or orthogonal to each other, for example, when a grass species or prey item has an equal chance of being grazed or captured in any habitat (May, 1975). The Summation method is used for dependent resources eg. where any grass species or prey item occurs in only one particular habitat, hence, there is a direct relationship between the presence of a grass species and a habitat type (May, 1975). Thus the choice of method depends largely on the type of resources or niche dimensions that one is considering.

The Product method calculates the product of the α's along each dimension,

$$\alpha ij^{p} = \prod \alpha ij(k) \text{ ....5.4}$$

where, αij^{p} is the product for species i and j, and ..ij(k) is the αij for the kth resource. One simply multiplies the two overlap coefficients for each different resource dimension.

The Summation method calculates the average of the Pik's along each dimension and takes the form;

$$\alpha ij^{s} = \frac{\sum \alpha ij(k) \text{ .....5.5}}{n}$$

where αij^{s} is tne summation for species i and j, and $\alpha ij(k)$ is the αij computed for tne k'th resource. This method generally overestimates true niche overlap, whereas multiplicative overall overlaps often underestimate true multidimensional overlap (Pianka, 1974). Furthermore, it is often difficult to judge whether resources are dependent or independent. Secondly, some resources may have subtle interdependence, such as use of time, use of food, and use of space (Slobodchikoff and Schulz, 1980). Thirdly, the degree of dependence or independence of particular resources may differ between the different species. The fourth problem, which was pointed out by May (1975), concerns tne inaccuracy of estimating multidimensional overlap coefficients from single resource dimensions. This is best illustrated by Figure 5.2 which depicts two (continuous) resource axes a and b, eg; food and foraging height, and two - dimensional utilization functions for the two species, 1 and 2. It is clear that although the species are non-overlapping when viewed along the single resource axes and overlap is depicted. Overlap measures for multidimensional resources may therefore be overestimated.

Finally, another problem which has not been mentioned in the literature, is the complex phenomenon of electivities for a

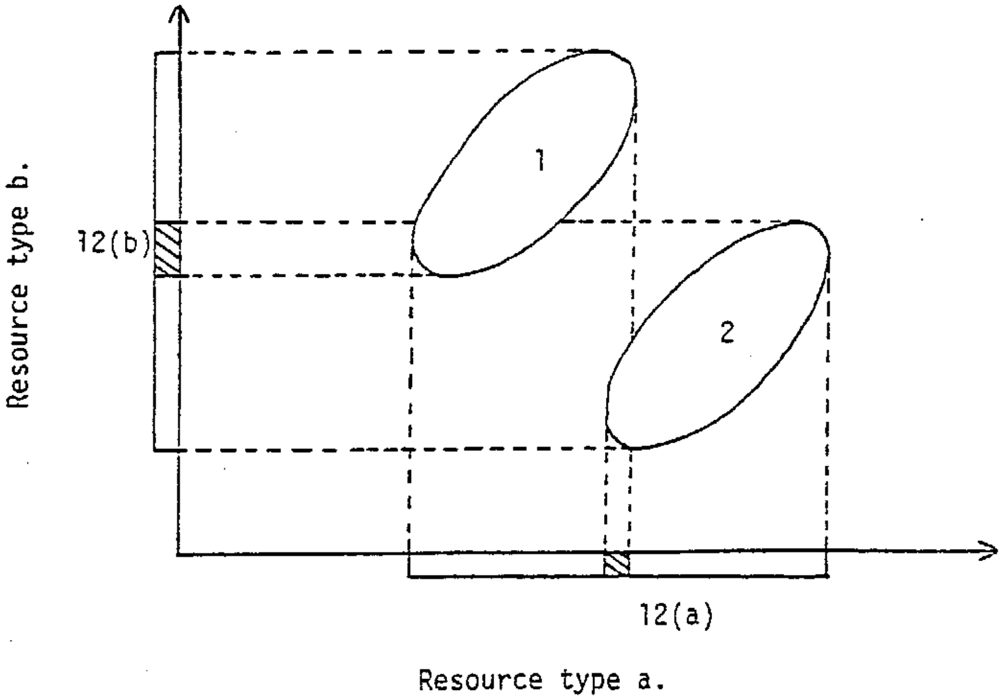


Figure 5.2 : Two non-competing species, 1 and 2, depicting overlap along the two single resource dimensions. (Adapted from May, 1975).

particular prey type differing in different habitat. For example, it has been observed that the white rhino population at Pilanesberg exhibit different dietary electivities in different habitats (refer to section 4.3.3). Consequently, the use of either the Summation or the Product methods in this case is inappropiate for determining overlap across several habitats. Rusterholz (1980), also realizing their limitations, used a combined method whereby he calculated the mean overlap of those dimensions which correlated with each other and multiplied this by the niche overlap along the potentially independent dimension. Although his method improves the estimate of true multidensional overlap it is by no means perfect. A modification of both the Asymmetrical and the Product methods has been proposed in an attempt to circumvent these problems.

When using the Asymmetrical or the Symmetrical methods, alphas for both the habitat and dietary dimensions are calculated separately. In other words, the dietary overlap coefficients between species 1 and species 2 are assumed to be equal throughout each habitat type. This is not correct if the dietary electivities of each herbivore species differs in each habitat. The modifications must therefore first calculate the dietary overlaps within each habitat type, and then incorporate the habitat overlaps for each herbivore (consumer) species. The two-dimensional overlap equation would therefore take the form;

$$\alpha\, ij = \sum_{n=1}^{n} \left[\left(\frac{\sum PikH \times PjkH}{\sum (PikH)^2} \right) \times \left(\frac{eiH \times ejH}{(eiH)^2} \right) \times aH \right] \quad ...55.6$$

where i,j = herbivore species,
H = habitat, 1...n,
k = plant species in diet, 1...s,
PikH = proportion of plant species k in species i's diet in habitat H,

e_{iH} = proportion of time that herbivore species i spent in habitat H, and

a_H = proportion of the total area made up by habitat H.

The first part of the equation calculates the dietary overlap within each habitat using the Asymmetrical method as proposed by Pianka (1973). This value is then modified or weighted, firstly by the habitat, overlap and secondly by the proportional area of that habitat. This method, termed the "Weighted Overlap" method, calculates values from 0 to 1, again 0 indicating no overlap, and 1 indicating complete overlap.

By using this approach one is incorporating the relationship between both the habitat and dietary selection. For example, species i may overlap greatly in diet with species j but, species j may spend less time in the habitat, thereby decreasing the potential overlap between them. This value is then modified by the proportional area of habitat 'H' in the reserve. Hence, the total overlap in the relatively smaller habitats are weighted less than those in the larger habitats. The new method proposed is, therefore, not so much a modification of the mathematical formulae as an alternative in the approach used to calculate resource overlap along multiple niche dimensions.

5.2.2.3 Reduced Dimensionality in the Measurement of Habitat overlap

Hutchinson's (1957) concept of the ecological niche as a n - dimensional hypervolume invites the use of multivariate statistical techniques. Rotenberry and Wiens (1980) stressed the advantage of such methods in being able to display highly correlated variables along independent axes representing what they termed, "proximate" niche dimensions. Two widely accepted techniques, namely, Principle Component Analysis (P.C.A.) and Discriminant Function Analysis (D.F.A.) have been used in niche analyses.

The major advantage of D.F.A. is that the Discriminant Functions can be used, firstly, to identify the axes of niche separation, and secondly, the dispersion of locations along these axes can be interpreted as representing niche width or specialization.

Levins (1968) initially stated that "niche dimensionality refers not to the number of biologically relevant factors on the environment,....but to the number of factors which serve to separate species". This led Cody (1968) and James (1971) to use D.F.A. to separate bird species according to habitat characteristics. However, recent applications to niche analyses appear to have been based on the papers by Green (1971, 1974) and Shugart and Patten (1972). Green (1971), used D.F.A. to identify significant ecological factors separating species in a multidimensional space. The standard deviation of discriminant scores as a measure of niche breadth, and the percent overlap of 50% probability ellipses a measure of niche overlap. Dueser and Shugart (1978, 1979), on the other hand, used the average distance of the observations for a species from the origin of discriminant space as a measure of niche exploitation or position relative to the average microhabitat available. The coefficient of variation of the distances from the discriminant origin was used as a measure of niche breadth. Indices of overlap were calculated using the planar area of overlap of concentration ellipses relative to their total area (Dueser and Shugart, 1979).

A controversial problem which arises when considering multivariate analyses of habitat use or niche space is whether to sample environmental variables at sites determined randomly, or to record the variables only where the organisms of interest were sited. Rotenberry and Wiens (1980, 1981), used the former method for generating a set of habitat vectors to be analysed by P.C.A. Cody (1968, 1978), James (1971), Green (1971, 1974), Shugart and Patten (1972), Ferrar and Walker (1974), Attwell (1975), M'Closky (1976), and Dueser and Shugart (1978, 1979), however, all used the latter method (ie, centers or singing perches within territories for birds, and successful collecting sites for molluscs and mammals) to identify locations for habitat sampling. Green (1971), when justifying his method of recording environmental variables only where the organisms (ie, molluscs) were found, cited Hutchinson's (1968) reasoning that the "presence of a species in a sample was more informative than its absence". Presence indicates that a species could live at the site, whereas absence could arise because, either the site was unsuitable, the species had not yet colonized the area, or because the species was missed in the sample even though it was a favourable site (Hutchinson, 1968). Carey (1981) and Wiens and Rotenberry (1981), however, argued that this technique may only be meaningful for sedentary forms, or when applied on a macroscopic scale. Mobile animals may in fact be found not only in marginal habitats but also, during high densities, in completely unsuitable habitats. Presence is therefore not indicative of habitat suitability. However, the author argues that if one records the sites only where the animals are observed to forage then all the sites measured are part of the species feeding niche.

The major difference between these two sampling techniques lies in the interpretations of the canonical space. If one accepts that the origin of canonical space represents the mean of the disriminant (or factor) scores, or the mean of all sites sampled, then the niche metrics will differ for each sampling method. In the first method, the origin gives a better estimate of the average microhabitat available. The second method, however, estimates only the average of the microhabitat utilized by the species, and consequently, is influenced by their relative abundances (Carnes and slade, 1982). Common species would contribute more to the determination of the mean than the rare species, and therefore, are more likely to be located near the origin of the canonical space.

When information is required on niche specializations or niche breadths, samples of species absence must be included. However, measurements of the sites where the organisms were present need only be recorded if interested in niche overlap. In this case one is primarily interested in the relationships between the different species, rather than between the species and their environment.

During this study samples were measured only at the sites where the herbivores were present in order to describe the microhabitat selection within the major habitats.

The data collected consisted of several groups (herbivore species) each comprising a number of individual sites characterized by a number of site attributes. The variables take the form of either measured (eg. grass height) estimated scores (eg. percentage herbaceous cover).

5.2.2.3.1 Discriminant Function Analysis

Discriminant Function Analysis (DFA) is a well known multivariate statistical technique originally developed by Fisher (1936) as a means of classification. The method separates populations or groups which are known to be difficult, on the basis of several characters or attributes. It is particularly useful in niche analysis because it reduces the number of criteria or dimensions used for discrimination before the interpretaion of species separation is necessary (Green, 1971; Ferrar, 1973).

The first step in this analysis is the combination of F-ratios for each variable so as to identify those variables for which the ratio of between species variance to within species variance is sufficiently large to enable discrimination between herbivore species (Ferrar and Walker, 1974). Secondly, a series of latent roots (discriminant functions) and vectors are extracted from the total data set. These discriminant functions express the difference between species in terms of a few common gradients of variation instead of the gradients represented by each of the individual variables. The latent roots then give the proportion of the total variance extracted with the vector of the variable weights indicating the degree to which each variable is associated with the discriminant function.

Discrimination between groups is therefore expressed in terms of a few common gradients which can be identified by those variable weights most strongly associated with each discriminant function (Ferrar and Walker, 1974). The next step then calculates a discriminant score for each site (feeding locality), by summing the products of the variable weights and their respective values. The mean of the discriminant scores for all sites for each species is known as the group or species centroid (Ferrar and Walker, 1974).

Discrimant Function Analysis finally provides a posteriori classification function which can be used to assess the extent of group overlap based on the site characteristics (Telford, 1982).

The program algorithm used for this analysis is that of Klecka (1975) and was performed using an S.P.S.S package (Nie, et al, 1975).

5.3 Results and Discussion

5.3.1 Calculation of Niche Overlap

The percentage time spent by the herbivores in each habitat and the percentage contribution of each grass species in their diet represent the two resource dimensions used to calculate pairwise overlap. The overlap measures were based on the proportional use of six habitats and 35 grass species. Emphasis has been placed on calculating overlap only for the dry season. This was for two reasons, firstly, because of the limited time available, and secondly, because this period is most unfavourable in terms of resource limitation. The importance of measuring overlap during the leaner periods has been stressed by Schoener (1982) as competition between species is most likely to occur during these periods.

5.3.1.1 Single Niche Dimensions

5.3.1.1.1 Habitat Overlap

Habitat overlap was calculated between the white rhino and the four associated large grazers for all seasons (Table 5.1). This was done using the Asymmetrical method presented by Levins (1968) and MacArthur (1972).
Pairwise overlap was generally high for the species, except during the dry season when the ungulates were more susceptible to stress. A decrease in habitat overlap was apparent, especially during the late-dry season when the zebra showed a high preference for the hillside savannas. These habitats, because of their steep slopes are largely inaccessable to the white rhinos. This high overlap between all grazers results from the high selection of all species for the secondary grasslands, valley savannas and thickets.

The overlap estimates indicate that the wildebeest frequent those habitats most similar to the white rhino, and the zebra,

Season	Rhino x Wilde	Rhino x Harte	Rhino x Zebra	Rhino x Impala
Fire	1.06* 0.79	0.80 0.65	0.87 1.09*	1.09* 0.92
Early Wet	0.93 0.92	1.00* 0.92	0.81 0.83	0.73 0.79
Late Wet	1.07* 0.89	1.02* 0.86	0.93 0.90	0.72 0.95
Early Dry	0.97 0.96	0.75 0.90	0.81 1.03*	0.74 0.57
Late Dry	1.09* 0.83	0.79 0.68	0.35 0.44	0.90 0.80

Table 5.1 : Seasonal differences in the habitat overlap values using the MacArthur-Levins' Asymmetrical measure. The pairwise overlap estimate relative to the white rhino (rw) is shown on the lower left, with the estimate relative to either the wildebeest (Wild), hartebeest (Hart), zebra or impala on the upper right, ie. wr, wh, wz or wi, respectively.

the least. Seasonal changes occurred between all species, especially between the white rhino and zebra and the white rhino and impala. The impala, because of their selection mainly for the valley savannas and thickets, tend to overlap the least.

To summarize, all the herbivores show a high degree of overlap with the white rhino, indicating similarities in their habitat use. However, both temporal and spatial differences may be occurring (Bell, 1969), which may affect the overall estimate. For example, herbivores may select similar habitats in different valleys or at different times.

5.3.1.1.2 Dietary Overlap

Dietary overlap between the white rhino and the other grazers was (as described earlier) determined only during the dry season, which is considered to be the period when food becomes a limiting resource.

The overlap measures for the diet were averaged for all habitat types, implying that similar diets were utilized in each habitat type. (The problems associated with this assumption was discussed earlier). The diet was estimated in each of the feeding sites mentioned in section 4.2.1.2.

When using the Asymmetrical method, overlap estimates are given both with respect to the white rhino and also with respect to the other four grazers (Table 5.2). In the first case, the proportion of resource type (k) in species i's diet, i.e. Pik, is that for the white rhino, and in the second, Pik is that for either hartebeest, wildebeest, zebra or impala. A number of points emerge from these measures. Firstly, those species selecting for a narrower dietary range than white rhino (e.g. hartebeest, zebra and impala) tend to have low overlap measures. Secondly, when measuring overlap with respect to a generalist (eg. white rhino which select for a wide variety of grass species), comparitively higher values are recorded, in some cases greater than one. (eg. 1.15 and 1.20).

Season	Rhino x Wilde	Rhino x Harte	Rhino x Zebra	Rhino x Impala
Early Dry	0.76 0.82	0.46 0.54	0.41 0.71	0.28 1.20*
Late Dry	0.80 0.59	0.76 0.64	0.40 1.15*	0.47 0.65

Table 5.2 : Seasonal differences in the dietary overlap values using the MacArthur-Levins' Asymmetrical measure. A similar key is used as in Table 5.1.

High overlap values were again recorded between the white rhino and wildebeest. Therefore, in terms of both the habitat and dietary niche dimensions, these species will most likely compete at high densities. Both the zebra and impala overlapped only slightly with the white rhino during the dry season. However, although they selected for similar habitats (see previous section), differences were apparent in their diet. However, whether these differences have resulted so as to avoid competition, as implied by Schoener (1974), is difficult to answer.

5.3.1.2 Multidimensional Overlap

Total niche overlap, based on both habitat and diet, was first determined using the two existing methods for calculating overlap on more than one dimension, i.e. the summation and product methods (Tables 5.3 and 5.4). Total overlap was then calculated using the proposed "weighted overlap" measure (Table 5.5).

With respect to the first two methods, the summation measure in all cases gave higher values than the estimates derived from the product method. However both the two methods indicate that wildebeest overlap the most with the white rhino and zebra the least. This was generally true throughout both the early and late dry seasons.

The "weighted overlap" method is based on the important condition that dietary selection differs between different habitat types. It first calculates dietary overlap in each habitat type and then subsequently modifies these by incorporating the habitat selection coefficients, thus giving rise to a more acceptable estimate. In this case dietary electivities, which are different in each habitat type can now be incorporated in the measures. The results are shown in Table 5.5.

Season	Rhino x Wilde	Rhino x Harte	Rhino x Zebra	Rhino x Impala
Early Dry	0.74 0.79	0.35 0.49	0.33 0.73	0.21 0.68
Late Dry	0.87 0.49	0.60 0.44	0.14 0.51	0.42 0.52

Table 5.3 : Total overlap based on both the habitat and dietary dimensions using the "Asymmetrical-Product method". A key similar to that described in Table 5.1 is used.

Season	Rhino x Wilde	Rhino x Harte	Rhino x Zebra	Rhino x Impala
Early Dry	0.87 0.89	0.61 0.72	0.61 0.87	0.51 0.89
Late Dry	0.95 0.71	0.78 0.66	0.38 0.80	0.69 0.73

Table 5.4 : Total niche overlap based on the habitat and dietary dimensions, using the "Asymmetrical-Summation method". See Table 5.1 for an explanation of the key used.

Season	Rhino x Wild	Rhino x Hart	Rhino x Zebra	Rhino x Impala
Early-Dry	0.56 0.36	0.25 0.21	0.33 0.36	0.16 1.12
Late-Dry	0.14 0.29	0.49 0.14	0.08 0.04	0.39 0.12

Table 5.5 : Estimates of total niche overlap using the "Weighted Overlap measure". Refer to Table 5.1 for an explanation of the key.

A marked decrease in the overlap values is apparent. For example, the overlap between the white rhino and zebra is now much lower, i.e. 0.36. than the estimates determined using the previous two methods. Differences as large as this can obviously greatly influence herbivore management. These differences can be explained in terms of the herbivores' feeding ecologies. For instance, if two animals utilize similar grass species, but forage in different habitats, then obviously overlap is going to be very low. Similarly, low overlap would also occur if the species forage in identical habitats, but on different grass species. The first case is analogous to the white rhino and zebra where the zebra, by spending approximately 80% of their time foraging in the inaccessible hillside savannas, show low overlap with the white rhino. When using the summation or product methods to calculate multidimensional overlap, fairly high measures (0.8 and 0.51, respectively) are observed as opposed to the "weighted overlap" measure(e.g. 0.04). In addition, another important aspect which must be considered is the dietary differences which are apparent between habitat types (see section 4.3.3). For instance, although the herbivores may depict similarities in their overall diet, the similar grass species may have been utilized in different habitats.

To conclude, the lower overlap values estimated using the "weighted overlap" method probably depict resource overlap more accurately. However all three methods need to be experimentally tested before definite conclusions can be made.

5.3.2 Habitat Overlap Using Discriminant Function Analysis

For the analysis all species recorded in less than ten sites were excluded because of their inadequate sample size. However, only four sites were recorded for impala, but were included out of interest as this species accounted for a large percentage of the total grazing ungulate biomass. Five herbivore species comprising a total of 110 feeding sites were analysed using DFA. An early dry and late dry season comparison was not possible as insufficient data were collected. Each feeding site was characterized using the habitat variables (e.g. grass cover, grass height and percentage bulk contribution of each of the 35 species) given in Appendix I.

The final analysis was carried out using a matrix of 5 species and 37 variables.

5.3.2.1 Variables capable of discrimination

Appendix J shows those variables for which the between group variance is large compared to the within group variance, measured by the partial univariate F-ratio. A variable is considered for selection only if its F-ratio is larger than a specified value. The partial F-ratio measures the discrimination introduced by the variable after taking into account the discrimination achieved by the other selected variables (Klecka, 1975, Hill, 1979). This therefore indentifies which variables are responsible for the separation of the herbivore groups, and the importance of each in this respect. All the variables are significant at the 1% level. The percentage abundance of Panicum deustum, Rhynchyletrum repens and Heteropogon contortus are related most closely with the occurence of herbivore species.

5.3.2.2 Dimensions of the Community Niche

The analysis produced four discriminant functions with the first three accounting for a total of 90% of the overall variace. Each discriminant function represents a gradient proportional in length to the percentage between species variance accounted for by each (Appendix K). Ferrar and Walker (1974) interpreted these trends of variance along the discriminant functions as representing the primary dimensions of a community niche.

In order to adequately describe the community niche dimensions, it is necessary to know the degree of association between the D.F.'s and each variable. Appendix K represents the degree of associations as standardised weights for each variable, with the highest positive (near the origin) and negative values (furthest from the origin) arranged in increasing magnitude (Ferrar and Walker, 1974).

The first and primary dimension (accounting for 49.6% of the total variance) represents a gradient from sites dominated by Panicum deustum (PADE) and Cymbopogon excavatus towards fairly tall grasslands dominated by Eragrostis gummiflua (ERGU) and Trichoneura grandiglumis (TRGR) The second discriminant function which accounts for 26.5% of the total variance suggests a trend from areas dominated by Loudetia flavida (LOFL), Digitaria eriantha (DIER) to areas dominated by Perotus patens (PEPA), Tristachya rehmanii (TRRE) and Eragrostis racemosa (ERRA). The third gradient which only accounts for 13,9% of the total variance, indicates a gradient from patches dominated by Cynodon dactylon (CYDA), Heteropogon contortus (HECO), Cymbopogon excavatus (CYEX) and Urochloa mosambicensis (URMO) to patches dominated by E. plana (ERPL), Tristachya rehmanii (TRRE) and Sporobolus pyramidalis (SPPY).

The remaining variance is due either to chance variability, or to variation in the individual variables that are not associated with the common trends (Ferrar and Walker,1974). None of the gradients could be interpreted with respect to the habitat types classified in chapter 3, although, the first axis may represent a gradient from thickets (dominated by Panicum deustum) at the one end, to secondary grasslands (dominated by E. gummiflua and Trichoneura grandeglumis), on the other. This suggests that the spatial separation of the herbivores is on a much finer scale than that discussed in chapter four.

5.3.2.3 Species Separation and Overlap along the Habitat Niche

Each herbivore's feeding site contributes to a discriminant score along each discriminant function. By plotting each discriminant score on the relevant D.F., scaled in proportion to the amount of variance extracted, it provides a multidimensional picture of the positions of each herbivore species' habitat niche (Figures 5.3 and 5.4). The extent and nature of species separation (or overlap) is represented by the distances between and location of the species centroids. Page and Walker (1978), interpret these centroids as indicating the species' niche centres. When considering the ecological separation or overlap of species one is more interested in their relative positions or patterns in the canonical space rather than their specific locations, ie., the degree to which two species separate or overlap. Figures 5.3 and 5.4 depict the species centroids and their variance on a two-dimensional space represented by the first three discriminant functions.

The first axis or discriminant function, representing a gradient from short grasslands dominated mainly by *Panicum deustum* and *Cymbopogon* excavatus to taller grasslands dominated by *Eragrostis gummiflua* and *Trichoneura grandiglumis*, showed separation only between the impala and wildebeest, and impala and hartebeeest. All the other grazers showed little separation. The white rhino showed similarities with all grazers, especially with the wildebeest and zebra. Thus on the one extreme we have the hartebeest specializing on the secondary grasslands, and on the other, the rest of the herbivores depicting little separation.

Separation on the second axis was again incomplete, especially between the white rhino, wildebeest and hartebeest. The zebra showed only slight similarities with the other herbivores, particularly with the impala.

The third gradient again depicts incomplete separation. However when analysed multidimensionally, only slight overlap between wildebeest and hartebeest, and wildebeest and rhino is depicted. it does separate those species which were not distinct along the previous two gradients. These results seem to support the

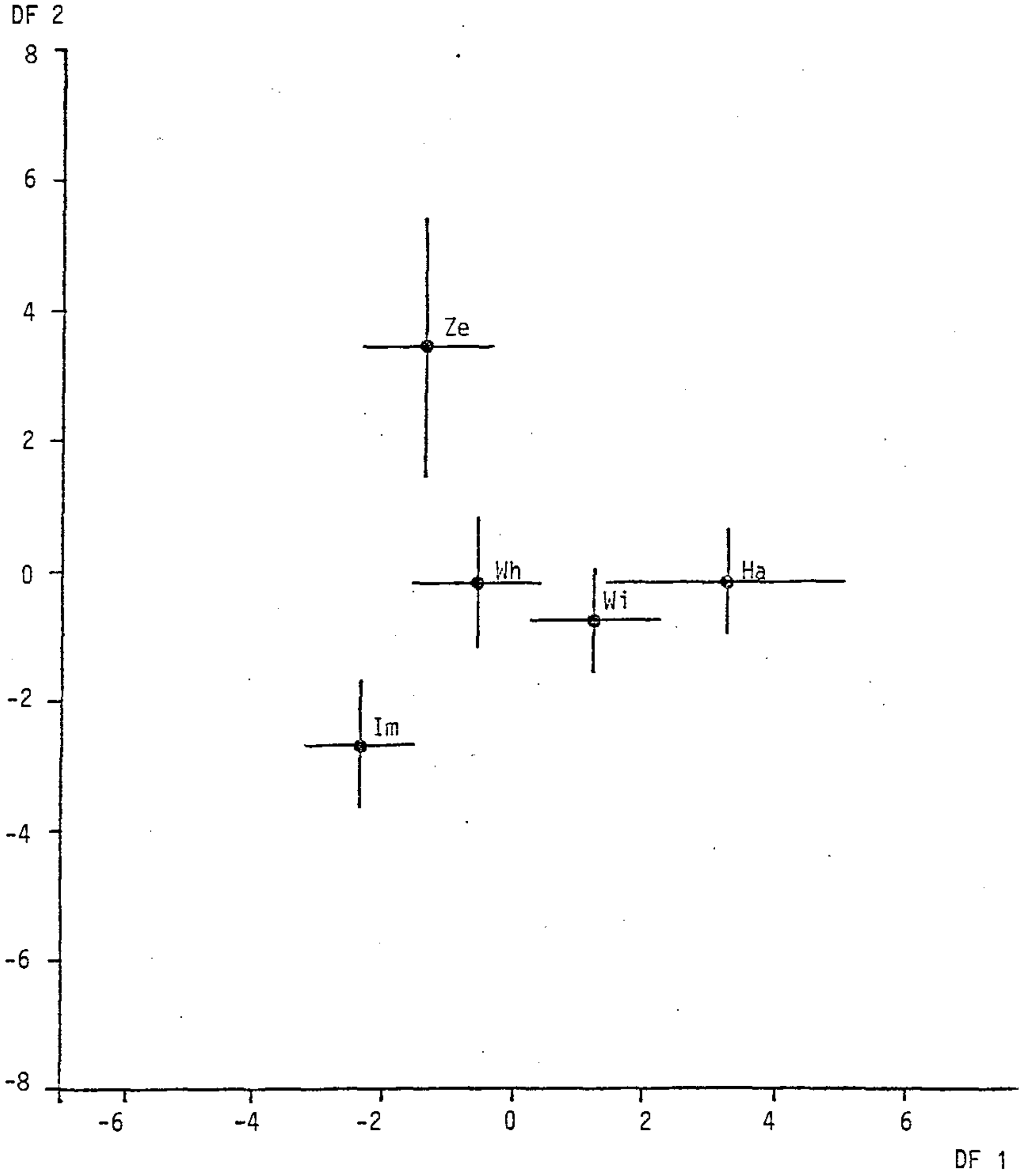


Figure 5.3 : Location of Species Centroids along DF 1 and DF 2 with two Standard Errors either side of the mean. (Wh = White rhino, Ha = Hartebeest, Wi = Wildebeest, Ze = Zebra and Im = Impala)

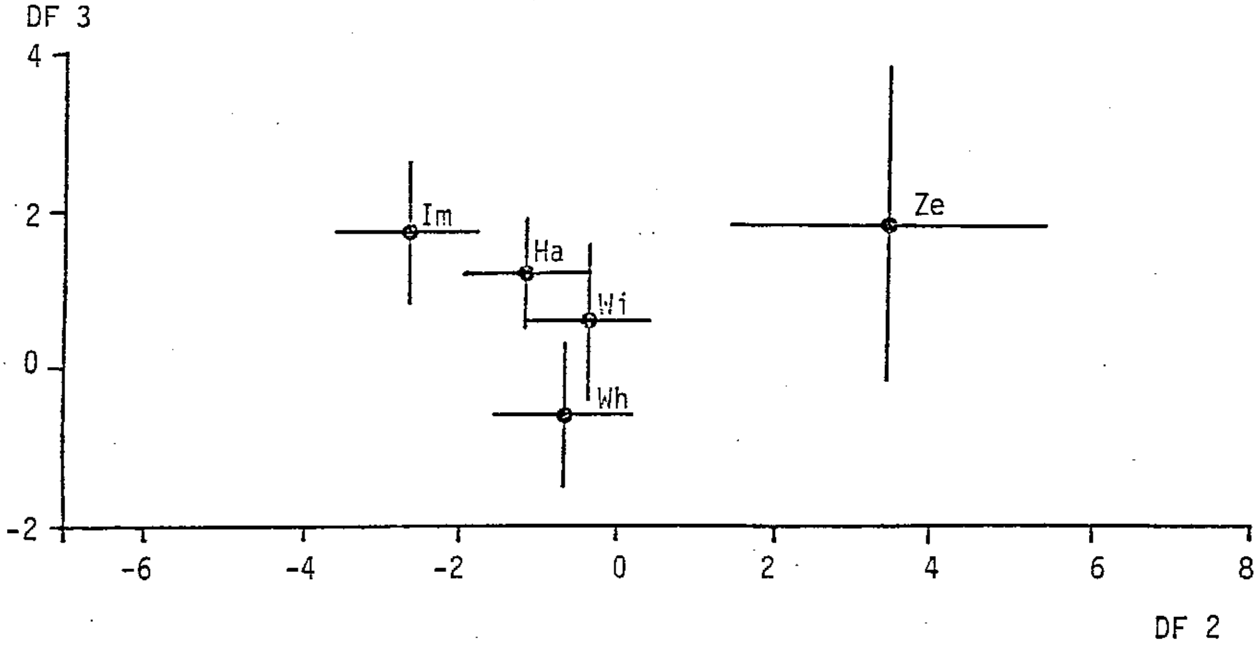


Figure 5. 4 : Location of Species Centroids along DF 2 and DF 3 with one Standard Error either side of the mean. (Wh = White rhino, Ha = Hartebeest, Wi = Wildebeest, Ze = Zebra and Im = Impala).

arguments given by May (1975) against calculating true multidimensional overlap from single dimensions.

Quantitative measures of habitat overlap, along these reduced dimensions, although possible (see Carnes and Slade, 1982), entail complex mathematical calculations. Hence, no quantitative measures were used to estimate habitat overlap. However, the analysis does point out two limitations of the previous methods. Firstly, true multidimensional overlap is generally overestimated, and secondly, species separation may occur at a more detailed level. Ferrar (1973), showed that niche separation was likely to take place on a basis of finer subdivisions (eg. diet), and not on the physical habitat structure per se.

5.3.3 Application of Niche Overlap in Calculating Stocking Densities in Multispecies Grazing Systems

The calculation of stocking densities in multispecies system requires information on not only the herbivores' feeding requirements, but also on their respective interactions. This applies particularly to grazing systems which are at or near carrying capacity or which are maintained at specific grazing levels. For example, if one wishes to add a herbivore into a reserve which has a low stocking density and abundant resources then no interactive effects will be evident. This is because the introduced animal has a negligible effect on the foraging behavior on the resident herbivores. The use of overlap measures become important only when concerned with systems at carrying capacity or when wishing to maintain specific grazing levels within these systems.

The importance of deciding on when a particular overlap value should be used becomes apparent when modifying stocking densities under particular grazing levels. If for example species 1 is the hartebeest and species 2 the white rhino, then the following question may arise when wishing to add a rhino in the reserve but still keeping the extent of utilization constant. How many hartebeest must be removed? When answering such a question, a decision must first be made on whether one is interested in the effect of species 1 on species 2 ($\alpha 21$) or, the affect of species 2 on species 1 ($\alpha 12$). This is best explained by thinking in terms of how the addition of a white rhino will affect the availability of the food for the hartebeest. In this case the affect of the generalist (white rhino) must be considered, hence, 0.46 ($\alpha 12$) hartebeest must be removed. If one wishes to add a hartebeest then 0.8 ($\alpha 21$) white rhino must be removed. When removing a white rhino (the generalist), then one can only add 0.46 ($\alpha 12$) hartebeest but, when removing a hartebeest then one can add 0.8 ($\alpha 21$) white rhino.

CHAPTER SIX

MEASUREMENT OF CARRYING CAPACITY IN A MULTISPECIES SYSTEM

6.1 Introduction

The concept of Carrying Capacity has been given much consideration in recent literature, and is generally defined as the state of equilibrium between herbivores and plants. The position of that equilibrium is indexed by its characteristic density of animals. In other words, it is the animal density at which the rate of forage production equals the rate of forage consumption (Caughley, 1979).

Sinclair (1981) on the other hand, argued that a population at carrying capacity should not be thought of as one with a stable or constant level. Rather, it is one that is fluctuating, often extensively between certain boundaries. He also stressed that we should be careful not to consider carrying capacity as an average of these random fluctuations - most systems are dynamic one way or another. Firstly, because half the time the population is above the average, and the rest of the time, below and secondly, because the fluctuations may be greater than 50% of the mean. He therefore concluded that in general, a population is at carrying capacity, or equilibrium, if it can persist while fluctuating within certain limits in that environment over a long period of time. The emphasis is therefore on persistence rather than steady state. In addition, it should be noted that although true carrying capacity is viewed as a long-term "equilibrium", in actual fact it consists of a number of short-term equilibria which change as a result of extraneous effects such as fluctuations in the environment, e.g. rainfall variation.

The concept and measurement of carrying capacity has been used widely, especially in range management, where guidelines on the maximization of livestock production are required. A number of workers have applied this concept to estimate the optimal stocking densities at which animals perform at their maximum growth rate on a particular range or habitat. Danckwerts (1982) for example, described the grazing capacity as the "productvity of the grazable portion of a unit of vegetation, which is the number of animal units that can be maintained per unit area of land in order to maximise animal production per unit input under consideration, but does not permit soil erosion or changes in the botanical composition....this would otherwise reduce the potential of the vegetation to produce animal products".

These agricultural estimates are based largely on surveys of plant densities, vegetative composition, rates of growth, proportions of annual growth removed by animals, and the time trends in these statistics. Their primary aim is to attain equilibria between plants and animals in order to provide maximum yield of wool, milk, meat or hides (Caughley,1976).

There are therefore two types of carrying capacities. The first, is the density of animals stocked at equilibrium with range conditions, which provide maximum sustained offtake or return, and the second is the density of animals that can be maintained indefinitely. The standing crop providing maximum sustained yield is lower than the maximum sustainable standing crop, because food per head must be kept high enough to generate productive yields (Caughley, 1976).

Although both describe equilibria between animals and vegetation, they are in actual fact two totally different kinds of equilibria (Caughley, 1979). The first differing from the second in its lower standing crop of animals and higher standing crop of vegetation. The agricultural carrying capacity is an equilibrium only because the animals are harvested to maintain a constant density.

The first equilibrium state, in which the net yield or harvest of animals is at a maximum, is termed the "economic carrying capacity". The second equilibrium, which is reached unaided, is known as the "ecological carrying capacity".

It is unfortunate that the difference between these two equilibria are not widely recognised. To the agriculturalist, the vegetation in systems above the economic carrying capacity are judged to be in "poor" condition and "overgrazed" when, in actual fact the system may be below its ecological carrying capacity. It therefore depends entirely on which equilibrium one is referring to.

The aim of this section is to determine the carrying capacity of the reserve for white rhinos at various stocking densities of associated grazers. The carrying capacity mentioned here is some point between the economic and ecological. The estimates obtained will be determined for average rainfall conditions.

6.2 Plant-herbivore Interactions

In order to get a clear understanding of the mechanisms leading to equilibria between two interacting populations (one being the herbivore or predator and the other the forage or prey type), it is important to monitor and analyze their population growth patterns.

Caughley (1979) identified three basic components of this process by which plants and herbivores reach a joint equilibrium;

(i) The growth response of the plants- the rate of increase of plant biomass as a function of the density of plants.
(ii) The functional response of the herbivores- the rate of intake per animal as a function of plant density.
(iii) The numerical response of the herbivores- the rate of increase per animal as a function of plant density (Caughley, 1976).

In grazing system of this type, the rate of change of herbivores is influenced only by the plant density, whereas the rate of change of plants is a function of both the herbivore and plant densities, i.e. the two components are interactive (Caughley, 1976).

The observed trajectory of a growing population can then be described by an equation that summarises the pattern of growth. Caughley (1976) proposed two different approaches. The first, although easier, but less useful, using curve fitting techniques, and the second, using models which simulate the two interacting populations.

The various population models, both simple (e.g. the logistic and delayed logistical equations) and complex (e.g. the interactive model of growth), have been examined in detail by May (1976) and Caughley (1976). The first two models have been rejected because they both treat vegetation and other resources as inert. The third model, the interactive model of growth, is considered to provide the best description of vegetation-herbivores systems. The equations presented below, are essentially those of May (1973) who used them primarily to model predator-prey system. Here they have been slipped down one trophic level (Caughley, 1976).

$$dV/dt = a_1 V\ (1 - V/k) - c_1\ N\ [1 - \exp\ (-d_1 V)] \ldots\ldots 6.1$$

$$dN/dt = N\ [-a_2 + c_2\ (1 - \exp\ (-d_2 V)] \ldots\ldots\ldots\ldots\ldots 6.2$$

where, a_1 = intrinsic rate of increase of plants,

K = maximum ungrazed plant density,

c_1 = maximum rate of food intake per herbivore,

d_1 = grazing (searching) efficiency of the herbivore when vegetation is sparse,

a_2 = rate at which herbivores decline when the vegetation is burnt or grazed flat,

c_2 = rate at which this decline is ameliorated at high plant density,

d_2 = demographic effiency of the herbivore; its ability to multiply when vegetation is sparse,

V = the vegetation biomass, and
N = the herbivore biomass.

The first equation expresses the rate of change of vegetation using two terms, the first depicting logistic growth, and the second, the rate of grazing. The second equation summarises the rate of change of herbivores (N) in terms of their intrinsic rate of increase, as modified by the availability of food.

Figure 6.1 (adapted from Caughley, 1976) depicts the trajectory of a population and its food supply growing as predicted by the above two interlinked equations. The herbivore biomass increases greatly as a result of the super-abundance of vegetation (commonly called an eruption), the vegetation biomass then decreases abruptly, followed by a dramatic reduction in the herbivore biomass (i.e. a crash) which then, converge to an equilibrium with their food supply, through dampened oscillations (Caughley, 1976). These two sets of oscillations are displaced from each other, the animals trailing behind the vegetation. This occurs as a result of the lag effects between the two populations.

Figure 6.2 (adapted from Caughley, 1976) is a phase diagram showing the changing ratio of animals to plants as the herbivore-plant system moves to its equilibrium point ($dV/dt = dN/dt = 0$) of N^*, V^*, a position that can be calculated as;

$$V^* = 1/d_2 \log e \; (c_2 \; / \; c_2 - a_2) \ldots\ldots\ldots\ldots 6.3$$

$$N^* = (V^* a_1 \; (1 - V^* / k)) \; / \; (c_1 \; (1 - \exp\,(-d_1 V^*))) \ldots 6.4$$

An interesting feature of the vegetative equilibrium is its complete independence of the variables of plant growth, the animals alone determining its level. The equilibrium level of the animals, on the other hand, is determined by the characteristics of both the plants and animals. (Refer to Caughley (1976) for a

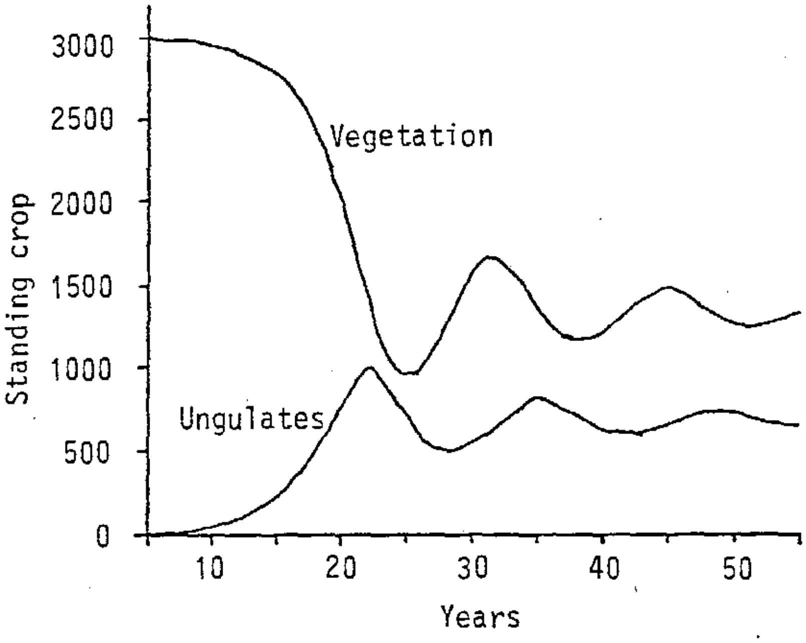


Figure 6.1 : Trends the vegetation and herbivore biomasses modeled by Caughley (1976).

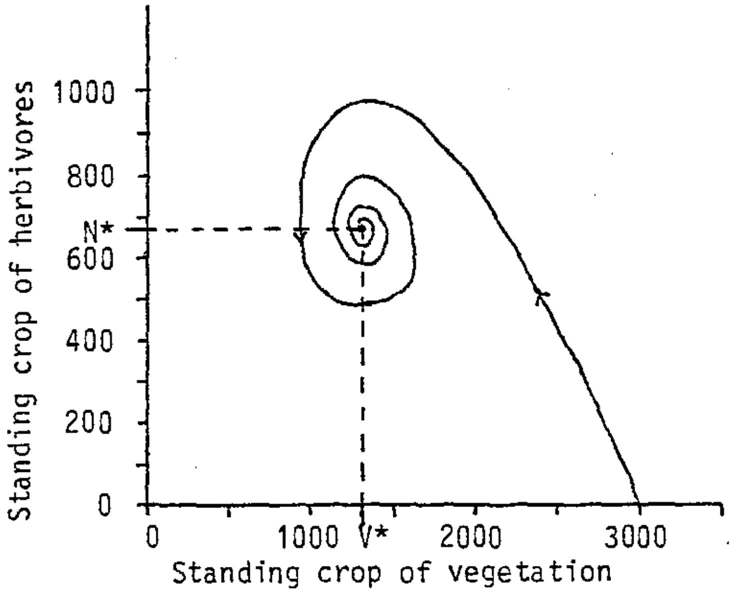


Figure 6.2 : Phases diagram of the relative densities of plants and herbivores as modelled by Caughley (1976).

more detailed explanation of these two interacting formulae).

Caughley (1976) identified three theoretical outcomes from the interactive model depending on the specific parameter values:

(a) Stable Equilibrium : the system returns to equilibrium when displaced from it.
(b) Stable limit cycle : instead of occupying a point equilibrium, the two populations occupy a closed cyclic equilibrium trajectory, the density of both plants and animals exhibiting well-defined periodic oscillations.
(c) Unstable equilibrium : when displaced from the equilibrium point the system oscillates with increasing amplitude until one of the components becomes extinct.

A fourth outcome, termed 'Chaos' has been identified by May (1976) which although bounded, does not settle into any cyclical patterns.

The last two outcomes identified by Caughley, and the additional one identified by May, are foreign to us, although it is becoming more apparent that they may exist; For example, the 4 year cycle of the lemmings in Alaska (Lack, 1954) and the long term fluctuations in the density of elephants in Zambia (Caughley, 1973). Both of these seem to reflect limit cycles between the herbivores and their food supply, though little conclusive evidence is available. The eruption and crash of the reindeer population on St. Matthew Island, as shown by Klein (1968), appear to take the form of an unstable system. Caughley (1976) concludes, that although limit cycles and unstable equilibria (and chaotic cycles) are theoretically possible, and may even have occurred in a few special instances, they are not really a feature of ungulate population dynamics. The main reason is that stable equilibria are least disruptive to both the plants and animals, so that systems of this nature would be selected for. Stable limit cycles and unstable equilibria, on the other hand, increase the probability of populations leading to extinction, and consequently, are selected against.

Unfortunately, Caughley's reasons given for the common occurrence of stable equilibria were largely based from a group selectionist point of view. It is highly unlikely that the populations interact in such a manner so as to always lead to stable equilibria. Instead, I believe that a system's dynamic behaviour is controlled largely by stochastic environmental events and its parameter and variable values.

This finally leads on to the question, of whether or not carrying capacity is a useful concept which can be applied to all systems. It is obvious that for systems, other than stable ones, the concept is extremely difficult to apply. However, for systems which are either stable or which can be managed, it becomes a useful concept. Therefore, before attempting to estimate the carrying capacity of any system, one must be fully aware of the dynamic interactions between the populations. One cannot assume that all systems will eventually become stable if left alone. The Pilanesberg grazing system is assumed to follow a stable cycle.

6.3 The Measurement of Carrying Capacity in a Multi-species Grazing System

For any effective management policies to be established, there is clearly a need to develop and refine predictive models, both for climatic variations and animal carrying capacities and protein production. Four different predictive models are described below.

6.3.1 The Rainfall-Metabolic Mass Relationship Method

It has been predicted that climatic variations, particularly in precipitation, affect the production of plant material, and hence the carrying capacity of the ecosystem (Coe, et al, 1976). Relationships of a predictive nature have been established between rainfall and primary production (e.g. Walter, 1954; Whittaker, 1970; Seely, 1978) and between actual evapotranspiration and primary production (Rosenzweig, 1968).

Associations have also been made between annual rainfall and large African herbivore biomass (Watson, 1972; Leuthold, 1973; Sinclair, 1974; Western, 1975; Phillipson, 1975, and Coe, et al, 1976). Coe, et al (1976) examined the relationships of both published and unpublished information on standing crop biomass of large herbivores and above ground net primary production (from mean annual precipitation). The hypothesis was proposed that for a majority of savanna systems, particularly those with rainfall less than 700mm, it is possible to establish "statistically significant relationships" which are able to predict large herbivore biomasses, and hence, their carrying capacities. They calculated a linear regression equation which could then be used to predict large herbivore biomasses from annual precipitation. The calculated regression equation for predicting long-term carrying capacities of semi-arid wildlife systems(Coe, et al, 1976), is;

$$\text{Large herbivore biomass} = 1.685(\pm\ 0.238)\ AP - 1.095(\pm\ 0.661) \quad ..6.4$$

By substituting the average rainfall for Pilanesberg (620mm) into the equation an estimate of 1 AU per 10 ha was obtained. This amounts to a total of 5350 AU in the reserve. (1 AU is equivalent to a large steer weighing 454kg).

6.3.2 The Standard Agricultural Method

The previous method calculates only the total large herbivore carrying capacity for an area. In most multispecies wildlife systems, such as the Pilanesberg Game Reserve, estimates have to by derived separately for each species. The "Standard Agricultural" method, commonly used for cattle systems, has been adapted for wildlife systems comprising of a number of species. The approach used in this method can be summarized as follows;

(i) the total carrying capacity for an area is first estimated using the relationship between rainfall and metabolic mass,

(ii) according to food availability, proportions of the total stocking density are allocated to each feeding class (Mentis and Duke, 1976, and Collinson and Goodman, 1981), and

(iii) finally, proportions of each feeding class are allocated to each of the species being considered.

The last two decisions are largely arbitrary, but do consider the following factors (Collinson and Goodman, 1981);

(i) the type of food and the proportion of each type available in the system,

(ii) the feeding habits (e.g. food type preference, land unit preference, habitat preference, and the tendency to overgraze selected sites) of the animals stocked or being stocked, and

(iii) the ecological and circumstantial objectives of the reserve.

The calculation of the total large herbivore biomass was discussed using the previous method. A stocking density of 1AU per 10ha, was recommended for a reserve with a similar rainfall pattern as that of Pilanesberg. However, as Collinson and Goodman (1981) noted, the range condition in Pilanesberg is generally poor, especially that of the pediment and valley bottoms. They therefore recommended a more conservative estimate of 1AU per 15ha.

Collinson and Goodman (1981) considered two major food types available to the herbivores. These were grasses and sedges in the herb layer, and forbs and woody plants. The range condition for each food type is then evaluated in terms of its quantity and quality, for each season, especially the winter months.

The herbivore species were then divided into four feeding classes, based on their feeding habits and preferred food types. The groupings recognized by Collinson and Goodman (1981), which essentially range from a continuum of grazers, to mixed feeders, and to browsers, are the bulk grazers (e.g. white rhino, buffalo, zebra), concentrate grazers (e.g. wildebeest, hartebeest, mountain reedbuck), mixed feeders (e.g. elephant, impala, eland)

and browsers (e.g. black rhino, giraffe, kudu).

The allocation of the total stocking density, firstly, to each feeding class, and secondly, to each species, was then calculated. As shown in Appendix N (adapted from Collinson and Goodman, 1981), a major portion (45% = 1470 AU's) of the total stocking density was allocated to the bulk grazers, because of their selection for the most abundant, low to moderate quality food source. The rest was then allocated to the other feeding classes, 20% (654 AU's) to the concentrate grazers, 20% (653 AU's) to the mixed feeders, and 15% (490 AU's) to the browsers. The recommended stocking density of white rhinos was 488 AU's or 200 animals.

The major problem with this technique is that the final stocking densities, estimated for each species, rely heavily on both the types of food resources available to the animals, and their preferences. Differences in any of these aspects would lead to differences in the carrying capacity assessments. In addition, by classifying the herbivores into feeding types they are assumed to have identical feeding patterns. This will obviously underestimate the values. The next two proposed methods attempt to calculate carrying capacity using the quantitative feeding data collected during the study. Finally, a model was developed which explores another important aspect similar to the one mentioned by Collinson and Goodman (1981), i.e. the tendency of species to overgraze selected sites, and its influence on carrying capacity estimates.

6.3.3 The Modified Agricultural Method

This approach differed from the previous method in two main aspects. Firstly, the grazing species permissible in the reserve, whether as a result of the habitat potential, or ease of availability (Mentis, 1977), was reviewed. Secondly, with the use of both habitat and dietary overlap coefficients (with respect to white rhino), the divisions of the herbivores into feeding types was unnecessary. Thus, the Standard Agricultural technique was modified based on the quantitative feeding data collected on the following grazers, in addition to the white rhino;

(i) wildebeest,
(ii) hartebeest,
(iii) zebra, and
(iv) impala.

The carrying capacity of the white rhinos, given various stocking densities of other grazers and their respective overlap coefficients (for the dry season only), were then calculated using the formula described below;

$$Q_r = \left[T - \left(\sum_{i=1}^{n} N_i \times C_i \Big/ A_i \right) \right] \times A_r \ldots.6.5$$

where, Q_r is the carrying capacity of the white rhino,

T is the total permissible grazing animal units of the white rhino, in the absence of other grazers,

i is the grazing animal species, 1......n,

N_i is the number of individuals of species i,

C_i is the total overlap coefficient between the white rhino and species i,

A_i is the animal unit equivalent for species i, and

A_r is the animal unit equivalent of white rhino.

In a multispecies grazing system such as Pilanesberg, caution must be taken when estimating the total permissible animal units in the reserve. Collinson and Goodman (1981) arrived at an estimate of 2124 grazing animal units (Appendix N). However, the total area of the reserve has been recently updated to 53500 ha (Peddie, 1983), as opposed to 49000 ha estimated by Collinson and Goodman (1981). The estimated flat area suitable for white rhino, is approximately 28000 ha thus permitting only a total of 1867 grazing animal units (approximately, 766 white rhino). The less dominant species, such as the buffalo (12), sable (14), waterbuck

(40), etc. (Appendix N), must also be accounted for. Approximately, 130 AU were allocated to these grazers. The mountain reedbuck were not included because of their almost total selection for the summit and hillside savannas. If the white rhino were the only major grazers in the reserve, then the total permissible animal units for this species would be 1737, i.e. approximately, 712 animals.

The present approximate densities of the four major associated grazers (1500 hartebeest, 1500 wildebeest, 1000 zebra and 3500 impala) and the respective overlap coefficients (averaged for the dry season) of 0.37, 0.35, 0.21 and 0.28, respectively were then substituted into equation 6.5. The carrying capacity of the white rhino, under the present stocking densities was calculated as 1011 AU's or approximately 415 animals. This value would obviously change if either the animal numbers or the species mix changes.

However, the final estimate, assuming that the animal densities and the overlap coefficients are accurately determined, relies heavily on the estimate of "T". In the above two methods it is assumed that this value has been accurately calculated. In a majority of cases this is not true.

6.3.4 The Modified Rainfall/Metabolic Mass Relationship

Coe, et al (1976) have pointed out the need for caution when relating rainfall directly to large herbivore biomass. Environmental factors such as the differences in topography, soil type and habitat type, can effect the primary production of an area. It is therefore imperative to analyze these aspects in detail before modifying the carrying capacity estimate obtained from the rainfall/metabolic mass relationship. This was the approach taken in this method.

First, the area under consideration must be divided up into habitat types. Then, depending on the size of the habitats and the mean annual rainfall, carrying capacity estimates are determined according to the relationship given by Coe, et al (1976). These estimates are now modified, firstly, by a topographical factor (T), secondly, by habitat preference factor (P), and thirdly, by a dietary importance factor (D). Therefore each habitat is weighted depending on its capability to support white rhinos. These weighted factors are calculated for each habitat based on the feeding preferences of the white rhino. For example, hilly areas would support a lower density of white rhino than areas of a less hilly terrain. Habitats dominated largely by unpalatable grass species would again support a lower white rhino carrying capacity than typical "sweetveld" areas dominated by palatable species. Table 6.1 summarizes the white rhino importance factors for each habitat type. These factors are then substituted into the following equation;

$$MCC = (ECC_h \times T_h \times P_h \times D_h) \text{........} 6.6$$

where, MCC is the modified carrying capacity of white rhino,

ECC_h is the estimated carrying capacity of white rhino, for habitat h, using Coe's, et al (1976) relationship,

T_h is the topographical factor for habitat h,

P_h is the preference factor for habitat h, and

D_h is the dietary importance factor of the plant species in habitat h.

All the factors range from 0 to 1 depending on their importance to the white rhino; 0 indicating unsuitable habitats and 1 indicating highly suitable. The topographical factor (T) was a given a value of 1 if the habitats were in the valley bottomlands, 0.1 (or near complete avoidance) if on the hill slopes and 0.5 for the other habitats. Values for the habitat preference factor (P) were based on the habitat preference indices discussed in chapter four. The habitat with the highest preference (during the dry season) was given a value of 1 (e.g. the thickets). The dietary importance factor (i.e. the ratio of the palatable to intermediate to unpalatable grass species) was given a value 1 if the dietary selection for a particular forage

Table 6.1 : Calculation of the White Rhino Carrying Capacity using the Modified Rainfall/Metabolic Mass Relationship. (T_h = Topographical Factor, P_h = Preference Factor and D_h = Diatary Importance Factor)

Estimated total area of reserve = 51500 ha.
Estimated area suitable for white rhino = 28000 ha.
Estimated carrying capacity = 1AU to 15 ha.
Rainfall = 620mm.

	Secondary grassland	Pediment grassland	Valley savanna	Hillside savanna	Thicket	Summit savanna
Area (ha)	3120	1630	7320	23366	7535	8500
Carrying capacity (ECC)	208	109	488	1558	502	567
T_h	1.0	1.0	1.0	0.1	1.0	0.5
P_h	0.9	0.7	0.8	0.1	1.0	0.4
D_h	0.7	0.6	0.7	0.9	0.9	0.7
Estimated carrying capacity (MCC_h)	153	50	307	16	530	100

Total permissible carrying capacity = 1156 AU's.
Carrying capacity of white rhino = 1156 - 720 = 436 AU's.

type was high, i.e. if the habitats supported a high proportion of palatable grass species and 0 is dominated by unpalatable species.

The carrying capacity estimate (1156 AU's) calculated using equation 6.6 was then substituted as "T" in equation 6.5. The new carrying capacity for white rhino was now estimated as 436 AU's or 175 animals. This is almost half of what was calculated using the previous method which estimated a white rhino grazing carrying capacity of 1011 grazing animal units. It is therefore recommended that a white rhino carrying capacity of 436 AU's be stocked in the reserve under the present grazing conditions. This estimate can be modified if either the relative herbivore densities are altered, or if the overall condition of the reserve increases.

The marked differences between these methods suggests the importance of taken strict caution when recommending carrying capacity stocking densities for multispecies systems.

The next section deals with another important aspect which was mentioned by Collinson and Goodman (1981), that of ability for herbivores to "overgraze" selected sites. For example, species which specialize in foraging in single patches or habitats throughout the entire year will exert a greater impact than species which show seasonal habitat differences.

6.4 The "Weighted Consumption" Model

6.4.1 Introduction and Aims

Studies involving complex ecosystems involve the analysis of a large number of ecological factors and their respective interactions. Ecological models are constructed for two different purposes (Maynard Smith, 1974), one practical and the other theoretical. Models with a practical purpose are called "simulations" and are used for predicting the behaviours of various factors in the hope that they conform to the real world. The second type of models are constructed as a means of generating hypotheses. These models, commonly known as "sensitivity models" are less detailed and are constructed based only on the major ecological principles (Maynard Smith, 1974). The finer details of the system are omitted. These models are useful in defining goals and priorities of research (Jones, 1976).

The number of animals which can be stocked in a reserve is a function of both the resource availabilty and the herbivores' feeding requirements. The previous section outlined the importance of four main aspects in influencing its assessment. These were the primary production, which is a function of rainfall, topography, habitat type, and forage type. A fifth aspect, which was mentioned by Collinson and Goodman (1981) is the tendency of grazers to remain foraging on a particular habitat which I will refer to as the "minimum grazing threshold". The herbivores are assumed to forage in a habitat until a critically low plant biomass is reached. This level will vary for different species depending on their feeding habits. It could also be referred to as a measure of the herbivores' tendency to disperse between habitats in a patchy environment. For example, impala have been observed feeding in heavily utilized areas practically devoid of grass cover. The minimum grazing threshold for this species would therefore be very low. The white rhino, because of its large body size and preference for short grasslands (see chapter 4), may be typical of species having low threshold levels. Zebra, on the other hand, tend to select for the taller grasslands with higher plant biomasses (chapter 4). These species are characteristic of grazers with fairly high threshold levels.

The importance of these species characteristic threshold levels becomes apparent when relating them to the habitat's acceptable level of condition, i.e. the level beyond which plant growth ceases. If a species minimum threshold level is below that of the habitat's acceptable condition, then it is likely that the habitat will be grazed beyond a level at which recovery can occur.

The aim of the model was to investigate the possible consequences of varying the minimum grazing thresholds on the habitat's conditions. The model was programmed using the Apple version of UCSD Pascal.

6.4.2 Structure of the Model

6.4.2.1 Overview

The model has been based largely on the field data collected during the study (refer to chapters 3 and 4). It simulates the amount of plant biomass available at the end of each season in response to different animal densities and minimum grazing levels. The model was constructed using a simple "supply and demand" approach, the supply being the availability of plant forage, and the demand being the herbivores' requirements.

The supply or availability of the plant biomass was calculated for the different forage types (i.e. palatable, intermediate and unpalatable) within each of the five habitats (i.e. secondary grasslands, pediment grasslands, valley savannas, hillside savannas and thickets). The initial standing crops in each habitat, except the hillside savannas which were estimated, were based on the biomasses calculated using the Board method discussed in chapter 3. The primary production during each season was estimated using the regression equation calibrated by Rutherford (1980).

$$\text{Primary Production} = -113.0 + 5.48\ \text{Rainfall} \quad \ldots\ldots\ldots 6.7$$

The rainfall data was generated either randomly or using actual figures measured in the reserve. Only actual rainfall data are used in the iterations.

The requirements of each herbivore species (e.g. white rhino, hartebeest, wildebeest, zebra and impala) was calculated as follows. First, the initial biomasses were read in. Then the consumption rates are calculated using the metabolic mass and daily intake relationship similar to that used by Sinclair (1977). The amount of plant biomass consumed from each dietary type in a habitat was calculated based firstly on the herbivores' habitat and dietary selection coefficients, (determined in chapter 4), and secondly on the white rhinos' minimum grazing thresholds.

The "condition indices" for each habitat were calculated by weighting each habitat and forage type by its importance to the white rhino. For instance the plant biomasses in the thickets will be weighted higher than the biomass in the hillside savannas. Similarly, the biomass of the palatable species are weighted higher than the unpalatable species. These weightings range from 0 to 1, 0 indicating poor condition and 1 indicating good condition. Table 6.2 summarizes these weighting factors. Although these condition indices are largely subjective, they do provide a means of gauging the impact of the herbivores under different conditions.

6.4.2.2 The Main Assumptions and Conditions

(i) The growth or production of the vegetation is driven by the rainfall alone.

(ii) The amount of grass biomass in a particular habitat cannot increase beyond a set maximum.

(iii) Competition between the grasses and between the grasses and trees does not inhibit grass production.

(iv) Previous grazing does not affect grass production.

(v) Only the five major herbivores can consume grass material.

(vi) Interspecific interactions between the herbivores occurs indirectly through the utilization of similar resources.

(vii) Movement between habitats is determined by the herbivores' distribution coefficients and their minimum feeding threshold levels.

(viii) The densities of the four associated grazers are fixed.

Table 6.2 : Weighting Coefficients (WC) used to estimate "habital condition". The Preference Indices (PI) for the forage type and habitat are calculated using equations similar to 4.5 and 4.6, respectively.

	Secondary grassland		Pediment grassland		Valley savanna		Hillside savanna		Thicket	
FORAGE TYPE	PI	WC	PI	WC	PI	WC	PI	WC	PI	WC
	1.5	0.6	1.5	0.6	2.0	0.8	0.0	0.0	2.5	1.0
Palatable	1.9	0.6	3.2	1.0	2.1	0.7	1.2	0.4	1.4	0.4
Intermediate	0.3	0.4	0.7	0.8	0.8	1.0	0.8	1.0	0.7	0.9
Unpalatable	4.0	1.0	0.3	0.1	0.3	0.1	0.0	0.0	0.0	0.0

$$\text{Habitat Weighting Coefficient} = \frac{\text{Preference Index for Habitat } h}{\text{Maximum Preference Index}}$$

$$\text{Dietary Weighting Coefficient}_h = \frac{\text{Preference Index for forage type } i}{\text{Maximum Preference Index for } i}$$

(ix) The annual cycle is divided up into four seasons, similar to those defined in chapter 4.

6.4.2.3 The Model

The model can be broken up into three major parts (see Figure 6.3). The first part calculates the plant biomass available to the herbivores at the beginning of each season. The second part calculates the total consumption of each forage type in each habitat. The third section then calculates the amount of biomass left over at the end of each season. Appendix M gives a listing of the program.

The amount of plant biomass available at the beginning of the season is calculated using the initial biomasses, read in (procedure READDATA) at the beginning of the program, and the production (procedure PRODUCTION) estimated from the Rainfall/primary production relationship. These values are then added together (procedure VEGETATION).

The amount consumed is then calculated for each forage type using the dietary preference indices determined for each species (procedure ANIMCONS). The total amount of plant biomass consumed by the herbivores is then subtracted from the amount available at the beginning of the season (procedure VEGCONS). These procedures calculate the total amount of plant biomass left at the end of the season.

The next part of the program concerns the comparison of these values with the minimum grazing threshold levels. If the amount of plant biomass left at the end of the season is less than the "minimum grazing threshold", then the program is re-run, but now using the modified distribution coefficients calculated in procedures MODMINDIST and MODDIST. These distribution coefficients are modified as follows. The animal biomass, in the habitat which has been grazed below the minimum threshold, is calculated so that only the minimum biomass is left at the end of

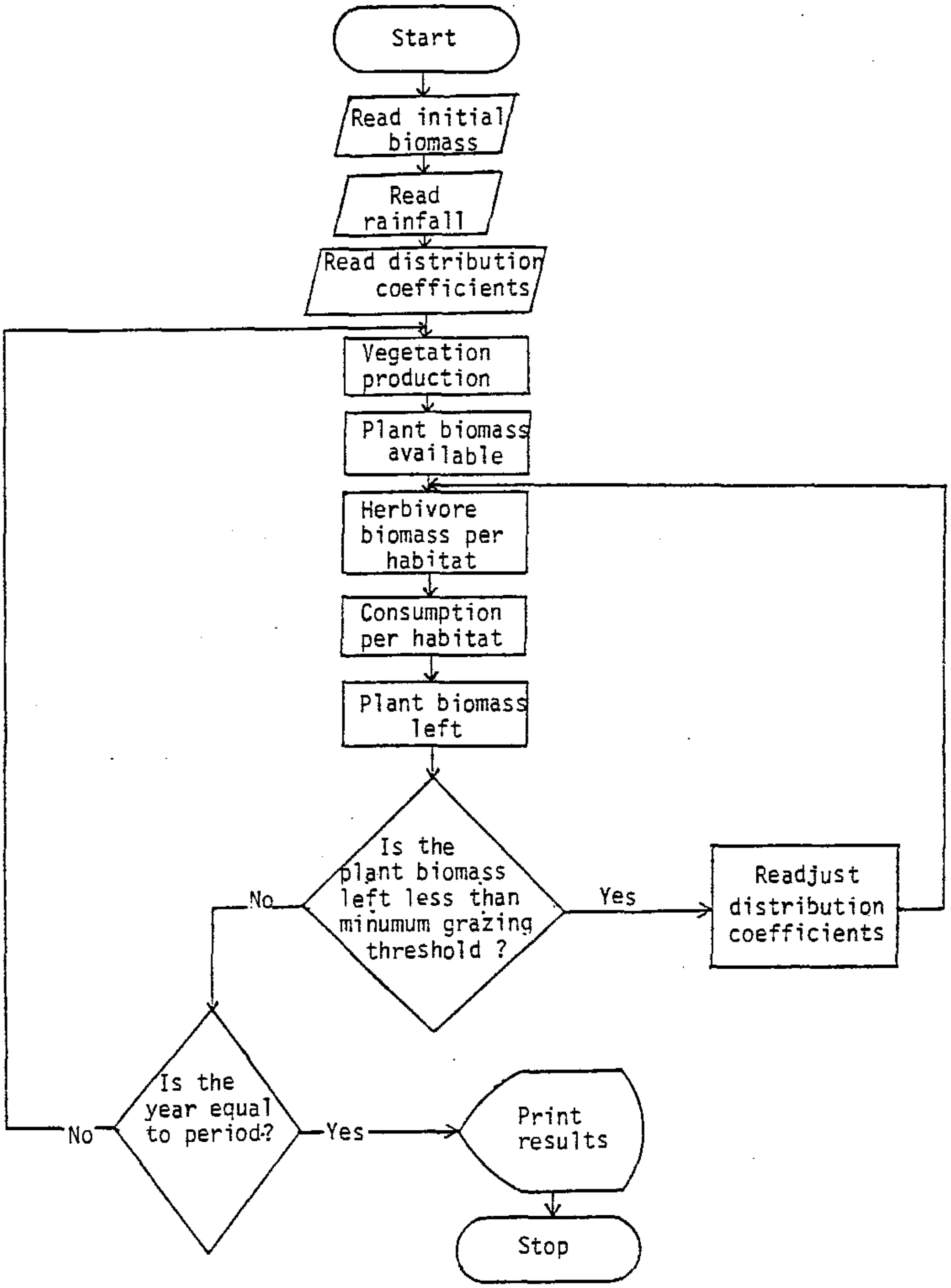


Figure 6.3 : Flow diagram illustrating the sequence of calculations for each seasonal interation of the model.

the season. The rest of the animal biomass is then allocated to the other four habitats depending on their relative importance to each of the herbivore species being considered. The program is now re-initialized using the new distribution coefficients. This whole process can be re-iterated until the year equals the period set prior to its run.

6.4.3 Results and Discussion

A series of iterations of the model were computed at 4 different white rhino biomasses (i.e. 2 kg/ha, 5 kg/ha, 10 kg/ha and 20 kg/ha) and 6 different minimum grazing threshold levels (i.e. 0.0 kg/ha, 50 kg/ha, 100 kg/ha, 150 kg/ha, 200 kg/ha and 250 kg/ha). The overall habitat condition (indices) at the end of a set time period (1 year) are presented in Figure 6.4.

The three-dimensional graph (Figure 6.4) illustrates the expected results under the different grazing conditions. In all cases the habitat condition deteriorated with increasing herbivore biomass (or density). This was expected as a greater offtake of plant biomass occurs at higher densities. The most notable feature however, was the influence of the minimum grazing thresholds at varying densities of white rhinos. At low white rhino biomasses (0.1×10^6kg) the importance of these levels is only slight. This can be explained by the fact that the consumption of the plant biomass by the herbivores at low densities is small relative to the primary production. However, as the herbivore biomass increases then the importance of the minimum grazing levels increases and the differences become more marked. At higher herbivore biomasses, consumption is very high. Therefore slight changes in their minimum threshold levels shows marked changes in the habitat's condition.

The main implications arising from these results become important when estimating carrying capacity densities of herbivores, which tend to select sites of low plant biomass. For example, species such as impala and white rhino will tend to show marked differences in their effects on the habitats as biomasses are

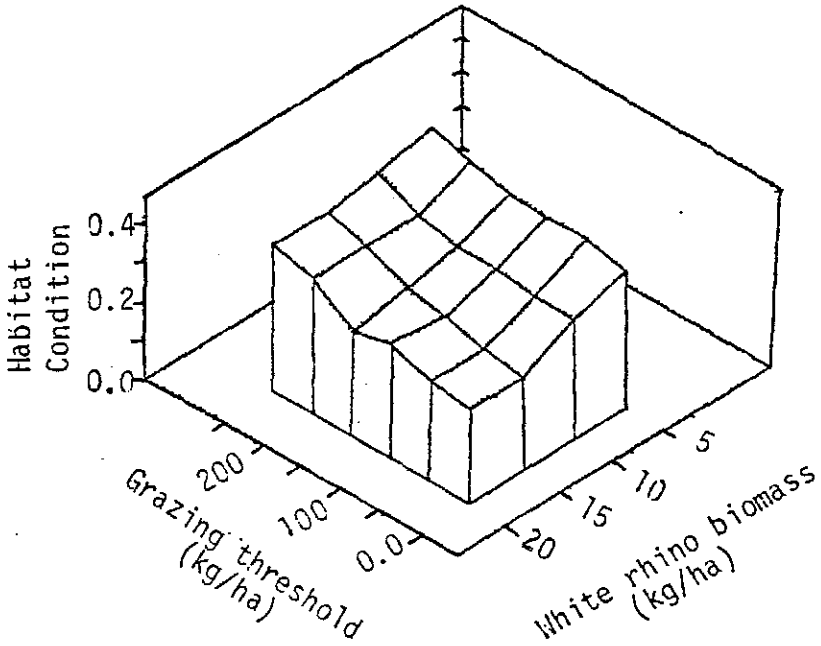


Figure 6.4 : A 3-dimensional graph depicting the relationships between white rhino biomass, the minimum grazing threshold and habitat condition.

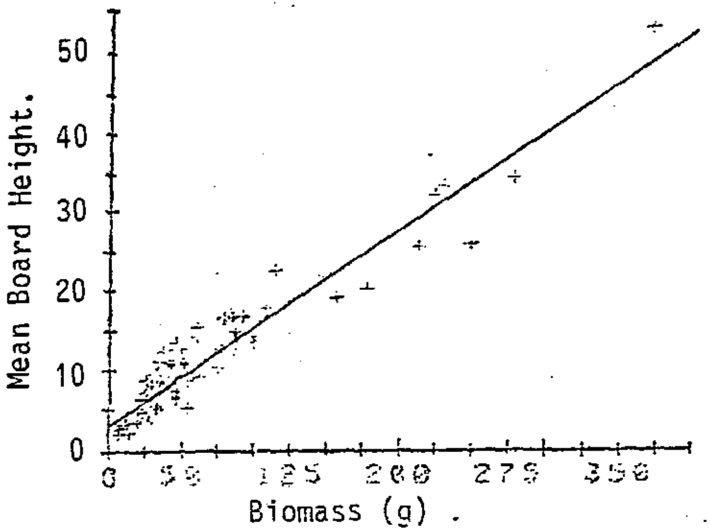
altered. Hence, these species will play a major role in influencing the habitats carrying capacity.

The model was simple in its approach so as to highlight the important aspects requiring further research. The next step therefore should be to create a more sophisticated model which would reflect the plant-herbivore systems more accurately. In addition, a better method of assessing the habitat's condition must be devised so that more realistic comparisons can be made with the real world.

APPENDIX A

Linear Calibration Curves Fitted to the Dry Weight of Grass and Board for the Two Major Seasons.

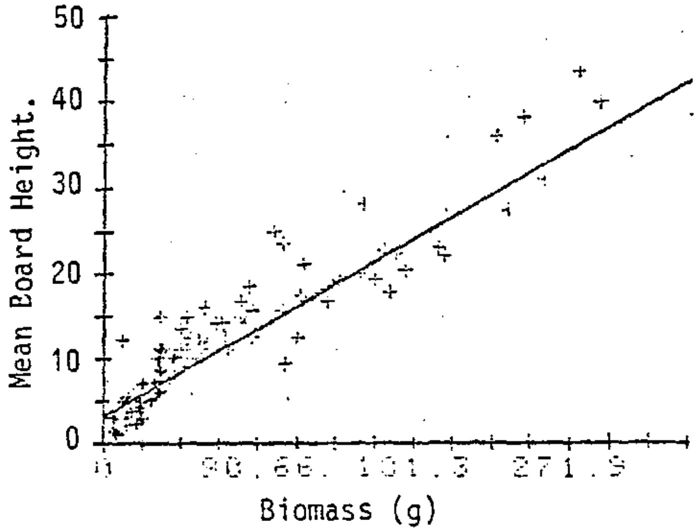
(a) Wet Season.



```
        LINEAR REG:CODE 1
SOUACE/DF       SS       MS       F
TOTAL 85    4720.8
REG     1   4305.8   4305.8 871.5
RESID 84     415.0        4.9
R SQUARE =          0.912

YHAT =      3.170+      0.109 X
```

(b) Dry Season.



```
   AOV: LINEAR REG:CODE 1
SOURCE/DF        SS       MS       F
TOTAL115     6416.6
REG     1    5322.2   5322.2 554.4
RESID114     1094.4        9.6
R SQUARE =          0.829
```

APPENDIX B

Results of Chi-square tests comparing seasonal differences in the habitat selection of all grazers. (* = Significant at the 5% level, ** = Significant at the 1% level and NS = No significance).

(i) White rhino.

	Fire	Early wet	Late wet	Early dry	Late dry
Fire	-	56.1**	55.1**	21.5**	15.0**
Early wet	-	-	7.5^{NS}	20.8**	58.0**
Late wet	-	-	-	5.8^{NS}	28.0**
Early dry	-	-	-	-	7.0^{NS}
Late dry	-	-	-	-	-

(ii) Hartebeest.

	Fire	Early wet	Late wet	Early dry	Late dry
Fire	-	0.0^{NS}	8.3^{NS}	101.1**	38.1**
Early wet	-	-	0.0^{NS}	101.1^{**}	30.0**
Late wet	-	-	-	387.1**	33.1**
Early dry	-	-	-	-	75.6**
Late dry	-	-	-	-	-

(iii) Wildebeest.

	Fire	Early wet	Late wet	Early dry	Late dry
Fire	-	12.0*	26.7**	12.5*	40.9**
Early wet	-	-	26.7**	5.0^{NS}	23.8**
Late wet	-	-	-	45.0**	75.9**
Early dry	-	-	-	-	45.9**
Late dry	-	-	-	-	-

APPENDIX B (cont.)

(iv) Zebra.

	Fire	Early wet	Late wet	Early dry	Late dry
Fire	-	40.8**	52.4**	66.0**	3524.8**
Early wet	-	-	0.0^{NS}	40.6**	25.5**
Late wet	-	-	-	64.8**	55.4**
Early dry	-	-	-	-	202.7**
Late dry	-	-	-	-	-

(v) Impala.

	Fire	Early wet	Late wet	Early dry	Late dry
Fire	-	0.0^{NS}	25.6**	44.8**	99.0**
Early wet	-	-	21.3**	36.8**	22.3**
Late wet	-	-	-	89.1**	57.8**
Early dry	-	-	-	-	31.4**
Late dry	-	-	-	-	-

APPENDIX C.

Results of Chi-square tests comparing seasonal differences in habitat selection between the white rhino and other grazers. (* = Significant at the 5% level, ** = Significant at the 1% level and NS = No significance).

(i) Fire.

	White rhino	Hartebeest	Wildebeest	Zebra	Impala
White rhino	-	45.0**	18.3**	11.4**	25.3**
Hartebeest	-	-	5.8^{NS}	122.8**	121.3**
Wildebeest	-	-	-	62.9**	65.3**
Zebra	-	-	-	-	21.3**
Impala	-	-	-	-	-

(ii) Early wet.

	White rhino	Hartebeest	Wildebeest	Zebra	Impala
White rhino	-	23.5**	42.3**	36.8**	197.3**
Hartebeest	-	-	21.3**	5.8^{NS}	121.3**
Wildebeest	-	-	-	7.5^{NS}	53.3**
Zebra	-	-	-	-	65.3**
Impala	-	-	-	-	-

(iii) Late wet.

	White rhino	Hartebeest	Wildebeest	Zebra	Impala
White rhino	-	83.9**	87.6**	101.8**	189.0**
Hartebeest	-	-	13.3**	12.5*	68.0**
Wildebeest	-	-	-	47.5**	48.0**
Zebra	-	-	-	-	85.3**
Impala	-	-	-	-	-

(iv) Early dry.

	White rhino	Hartebeest	Wildebeest	Zebra	Impala
White rhino	-	396.4**	28.5**	80.8**	166.4**
Hartebeest	-	-	94.1**	183.1**	289.0**
Wildebeest	-	-	-	104.8**	214.4**
Zebra	-	-	-	-	143.0**
Impala	-	-	-	-	-

(v) Late dry.

	White rhino	Hartebeest	Wildebeest	Zebra	Impala
White rhino	-	53.9**	13.8**	204.0**	39.8**
Hartebeest	-	-	117.9**	1577.7**	43.3**
Wildebeest	-	-	-	267.7**	71.7**
Zebra	-	-	-	-	284.7**
Impala	-	-	-	-	-

APPENDIX D.

Results for Student's t-test comparing seasonal differences in the forage type selection by white rhino. (* = Significant at the 5% level, ** = Significant at the 1% level and NS = No significance).

(i) Palatable species.

	Fire	Early wet	Late wet	Early dry	Late dry
Fire	-	1.6^{NS}			
Early wet	-	-	1.2^{NS}		
Late wet	-	-	-	1.8*	
Early dry	-	-	-	-	1.0^{NS}
Late dry	-	-	-	-	-

(ii) Intermediate species.

	Fire	Early wet	Late wet	Early dry	Late dry
Fire	-	1.8*			
Early wet	-	-	0.4^{NS}		
Late wet	-	-	-	1.4*	
Early dry	-	-	-	-	1.0^{NS}
Late dry	-	-	-	-	-

Results for Student's t-tests comparing differences in forage type selection between the white rhino and other grazers during the dry season. (** = Significant at the 1% level, * = Significant at the 5% level and NS = No significance).

(i) Palatable species.

	White rhino	Hartebeest	Wildebeest	Zebra	Impala
White rhino	-	2.8**	1.8*	0.7^{NS}	0.1^{NS}

(ii) Intermediate species.

	White rhino	Hartebeest	Wildebeest	Zebra	Impala
White rhino	-	2.9**	1.9*	0.5^{NS}	0.2^{NS}

APPENDIX F

Key to the grass species utilized by the Pilanesberg grazers

Mnemonic	Species
CYDA	*Cynodon dactylon*
RHRE	*Rhynchyletrum repens*
HECO	*Heteropogon contortus*
THTR	*Themeda triandra*
ERCU	*Eragrostis curvula*
ERSU	*E. superba*
ERRI	*E. rigidior*
ERGU	*E. gummiflua*
HYHI	*Hyparrhenia hirta*
BOIN	*Bothriochloa insculpta*
BRSE	*Brachiaria serrata*
URMO	*Urochloa mosambicensis*
LOFL	*Loudetia flavida*
DIER	*Digitaria eriantha*
PADE	*Panicum deustum*
PACO	*P. coloratum*
SPPY	*Sporobolus pyrimedalis*
UNPA	Unpalatable species, eg. *Elyonuris argenteus*, and *Cymbopogon* species

APPENDIX G

SEASON	HABITAT	CYDA		RHRE		HECO		THTR		ERCU		ERSU		ERRI		ERGU		HYHI		BOIN	
		PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI
Fire	VALSAV	43.1	7.0	0.0	0.0	21.6	1.4	1.9	0.4	1.9	0.8	10.4	4.3	5.6	2.7	0.0	0.0	6.3	1.3	0.0	0.0
	SECGLD	0.5	0.1	2.6	0.3	20.9	1.4	0.6	0.2	6.7	8.6	14.5	1.5	1.1	0.2	6.0	8.6	31.8	4.0	0.0	0.0
Early wet	VALSAV	0.0	0.0	0.0	0.0	24.5	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	36.5	7.4	0.0	0.0
	SECGLD	0.4	0.1	6.6	0.7	10.6	0.7	0.9	0.2	5.0	1.2	23.5	2.5	2.0	0.3	0.0	0.0	14.9	1.9	0.0	0.0
Late wet	VALSAV	5.4	0.9	0.4	0.1	34.7	2.2	2.7	0.6	5.4	6.4	6.9	2.9	5.4	2.6	0.0	0.0	5.4	1.1	0.0	0.0
	CYPAT	6.8	9.7	1.0	0.4	4.7	0.5	1.2	2.0	6.4	0.9	2.6	0.3	6.2	0.7	0.0	0.0	0.5	0.3	2.7	1.4
Early dry	VALSAV	1.1	0.2	1.7	0.5	34.3	2.2	14.3	2.9	1.5	0.6	0.7	0.3	4.0	1.9	0.0	0.0	7.1	1.4	1.8	2.3
	SECGLD	0.7	0.1	6.4	0.7	31.5	2.1	2.7	0.7	0.0	0.0	1.4	0.1	2.0	0.3	0.0	0.0	0.7	0.1	0.0	0.0
	CYPAT	0.0	0.0	9.0	3.2	32.6	3.7	1.4	2.3	4.8	0.7	10.7	1.3	6.7	0.7	0.0	0.0	3.7	2.5	0.0	0.0
	THICKET	2.9	0.2	7.0	35.0	4.9	0.9	0.0	0.0	10.4	2.4	0.0	0.0	5.2	2.7	0.0	0.0	0.0	0.0	0.0	0.0
Late dry	VALSAV	0.8	0.1	0.0	0.0	27.4	1.7	4.6	0.9	6.3	2.6	0.0	0.0	1.3	0.6	1.3	3.3	15.7	3.2	0.0	0.0
	SECGLD	3.2	0.3	18.3	1.9	12.5	0.8	0.0	0.0	0.0	0.0	30.8	3.3	9.4	1.6	0.0	0.0	0.0	0.0	0.0	0.0

Appendix : Percentage Contribution in the diet (PC) and Preference Indices (PI) for grasses eaten by white rhinos, by habitat and season. A key to the grass species is given in Table 4.1

(PAL, INT and UNP are the proportions of palatable, intermediate and unpalatable grass species, respectively).

SECGLD = Secondary grasslands.
VALSAV = Valley savannas
THICKET = *Acacia* and riverine thickets
CYPAT = *Cynodon dactylon* "lawns"

n = Number of transects.

SEASON	HABITAT	BRSE		URMO		LOFL		DIER		PADE		PACO		SPPY		UNPA					
		PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PAL	INT	UNP	n
Fire	VALSAV	0.0	0.0	0.0	0.0	0.0	0.0	2.4	1.5	0.0	0.0	0.0	0.0	0.0	0.0	6.7	0.2	33.9	59.4	6.7	6
	SECGLD	0.5	0.5	2.6	0.6	0.0	0.0	0.8	0.3	0.0	0.0	0.0	0.0	0.0	0.0	11.4	2.1	39.1	48.5	11.7	9
Early wet	VALSAV	0.0	0.0	0.0	0.0	0.0	0.0	4.2	2.6	0.0	0.0	0.0	0.0	4.2	10.5	30.7	0.9	24.5	44.8	30.7	4
	SECGLD	7.4	6.7	12.0	2.3	0.0	0.0	0.0	0.0	1.7	8.5	0.0	0.0	8.2	2.4	6.6	1.2	56.1	37.3	6.6	9
Late wet	VALSAV	0.0	0.0	15.1	8.9	0.0	0.0	0.4	0.3	3.1	3.4	0.0	0.0	5.0	12.4	0.0	0.0	62.0	38.0	0.0	6
	CYPAT	1.0	5.0	36.5	2.1	0.0	0.0	6.8	9.7	18.3	18.3	4.7	1.6	0.4	0.4	5.4	2.3	69.0	25.6	5.4	10
Early dry	VALSAV	7.5	8.3	2.9	1.7	0.0	0.0	8.7	5.4	8.1	9.0	4.8	1.9	0.0	0.0	1.4	0.1	72.6	26.0	1.4	9
	SECGLD	25.8	23.5	10.2	2.1	0.0	0.0	11.5	4.6	10.8	10.8	0.0	0.0	0.0	0.0	2.0	0.4	82.4	15.6	2.0	4
	CYPAT	0.0	0.0	8.4	0.5	0.0	0.0	0.0	0.8	20.2	20.2	2.5	0.9	0.0	0.0	0.0	0.0	75.5	24.5	0.0	4
	THICKET	0.0	0.0	4.4	0.4	0.0	0.0	0.5	0.1	44.9	6.2	17.1	2.0	0.0	0.0	0.0	0.0	71.3	28.7	0.0	5
Late dry	VALSAV	0.0	0.0	2.0	1.2	0.0	0.0	9.1	5.7	16.0	16.0	14.5	5.8	0.0	0.0	1.0	0.1	64.5	24.5	1.0	5
	SECGLD	0.0	0.0	5.8	1.2	0.0	0.0	2.7	1.1	6.3	6.3	3.2	3.2	0.0	0.0	0.0	0.0	58.6	41.4	0.0	4

Appendix : (continued)

APPENDIX H

Seasonal changes in the Percentage Contribution in the diet, of the grass species for the other larger grazers. A key to the grass species is given in Appendix F.

Species	Hartebeest		Wildebeest		Zebra		Impala	
	Early PC PI	Late PC PI	Early PC PI	Late PC PI	Early PC PI	Late PC PI	Early PC PI	Late PC PI
CYDA	0.1(1.0)	1.0(0.3)	1.0(3.5)	3.4(0.8)	0.0(0.0)	0.0(0.0)	5.0(8.3)	11.5(4.1)
RHRE	31.1(24.2)	15.7(6.7)	14.6(17.0)	18.1(4.2)	0.6(0.9)	0.6(0.9)	0.0(0.0)	0.0(0.0)
HECO	13.1(13.7)	12.5(3.8)	30.6(25.9)	6.4(6.4)	29.1(28.3)	56.0(8.9)	0.5(5.1)	6.3(2.5)
THTR	8.4(17.0)	9.0(4.7)	0.0(0.0)	10.2(1.0)	2.3(2.2)	9.6(3.8)	11.1(14.2)	17.2(7.1)
ERCU	1.0(3.1)	2.7(0.8)	8.1(4.8)	4.7(1.2)	0.0(0.0)	0.0(0.0)	7.5(4.5)	10.9(2.2)
ERSU	5.5(8.7)	4.5(2.4)	9.4(10.1)	4.3(2.5)	32.0(19.1)	0.0(0.0)	0.0(0.0)	4.7(1.9)
ERRI	3.7(5.3)	1.4(1.4)	4.8(4.5)	3.8(1.1)	0.0(0.0)	0.0(0.0)	2.5(1.6)	2.8(0.8)
ERGU	3.4(9.8)	9.6(2.7)	0.2(10.7)	1.0(2.6)	0.0(0.0)	0.0(0.0)	0.0(0.0)	0.0(0.0)
HYHI	8.3(11.3)	10.4(3.1)	0.7(9.3)	11.5(2.3)	0.0(0.0)	0.0(0.0)	0.0(0.0)	3.6(1.5)
BOIN	0.0(0.0)	0.0(0.0)	2.2(8.7)	0.4(2.1)	0.0(0.0)	0.0(0.0)	0.0(0.0)	0.0(0.0)
BRSE	15.5(19.9)	1.6(5.5)	7.6(4.2)	7.2(1.0)	5.2(3.2)	13.0(5.0)	0.0(0.0)	0.0(0.0)
URMO	2.5(5.6)	4.5(1.5)	4.7(4.5)	9.4(1.1)	0.0(0.0)	0.0(0.0)	1.5(1.2)	1.0(0.6)
LOFL	0.0(0.0)	1.6(2.0)	0.0(0.0)	0.0(0.0)	0.0(0.0)	10.6(5.4)	0.0(0.0)	0.0(0.0)
DIER	2.8(11.1)	16.0(3.0)	7.0(9.0)	5.1(2.2)	13.4(7.5)	0.8(2.3)	0.0(0.0)	11.5(4.7)
PADE	0.0(0.0)	0.0(0.0)	3.0(4.7)	5.5(1.1)	0.0(0.0)	0.0(0.0)	74.9(B0.7)	26.6(15.3)
PACO	1.0(7.2)	1.0(8.5)	5.7(2.5)	0.0(0.0)	0.0(0.0)	0.0(0.0)	0.0(0.0)	0.0(0.0)
SPPY	0.0(0.0)	1.6(0.5)	2.0(4.0)	3.3(1.0)	0.0(0.0)	8.8(2.8)	8.0(6.6)	4.2(3.3)
UNPA	0.0(0.0)	0.0(0.0)	0.0(0.0)	0.0(0.0)	0.0(0.0)	0.0(0.0)	0.0(0.0)	0.0(0.0)

APPENDIX I

Summary of the 37 variables and their mnemonics used in the multivariate analysis.

No.	Mnemonic.	Variable.
1	COVER	Percentage aerial cover of herbaceous layer.
2	HEIGHT	Average height of herbaceous layer.
3	CYDA	% cover *Cynodon dactylon*.
4	ARCD	% cover *Aristida congesta*.
5	RHRE	% cover *Rhychelytrum repens*.
6	HECO	% cover *Heteropogon contortus*.
7	THTR	% cover *Themeda triandra*.
8	ERCU	% cover *Eragrostis curvula*.
9	ERSU	% cover *E. superba*.
10	ERRI	% cover *E. rigidior*.
11	ERRA	% cover *E. racemosa*.
12	ERPL	% cover *E. plana*.
13	ERGU	% cover *E. gummiflua*.
14	ELAR	% cover *Elionuris argenteus*.
15	CYEX	% cover *Cymbopogon excavatus*.
16	HYHI	% cover *Hyparrhenia hirta*.
17	TRGR	% cover *Trichoneura grandeglumis*.
18	BOIN	% cover *Bothriochloa insculpta*.
19	TRRE	% cover *Tristachya rehmanii*.
20	SEFL	% cover *Setaria flabellata*.
21	BRSE	% cover *Brachiaria serrata*.
22	BRNI	% cover *B. nigropedata*.
23	URMO	% cover *Urochloa mosambicensis*
24	LOFL	% cover *Loudetia flavida*.
25	DIER	% cover *Digitaria eriantha*.
26	DIAM	% cover *Diheteropogon amplectans*.
27	TRBE	% cover *Tragus berteronianus*.
28	PADE	% cover *Panicum deustum*
29	PACO	% cover *P. coloratum*.
30	POSQ	% cover *Pogonarthria squarrosa*.
31	SPPY	% cover *Sporobolus pyramidalis*.
32	CHVI	% cover *Chloris virgata*.
33	SENI	% cover *Setaria nigrirostris*
34	SPAF	% cover *Sporobolus africanus*
35	PEPA	% cover *Perotus patens*.
36	ERCR	% cover *Eragrostis* species
37	DISM	% cover *Digitaria smutsii*.

APPENDIX J

The univariate F ratios with percentage levels of probability for each of the 37 variables.

Variable	Wilks' Lambda	Univariate F ratio	Probability
COVER	0.91975	2.290	0.0645
HEIGHT	0.90303	2.819	0.0288
CYDA	0.89417	3.107	0.0185
ARCO	0.88196	3.513	0.0098
RHRE	0.79250	6.873	0.0001
HECO	0.82701	5.491	0.0005
THTR	0.94545	1.515	0.2032
ERCU	0.95965	1.104	0.3588
ERSU	0.96833	0.858	0.4915
ERRI	0.97159	0.767	0.5486
ERRA	0.99234	0.202	0.9364
ERPL	0.99634	0.096	0.9834
ERGU	0.87882	3.620	0.0083
ELAR	0.98265	0.463	0.7624
CYEX	0.96889	0.842	0.5011
HYHI	0.95076	1.359	0.2531
TRGR	0.95076	1.502	0.2069
BDIN	0.97824	0.583	0.6750
TRRE	0.81731	5.868	0.0003
SEFL	0.96116	1.061	0.3798
BRSE	0.87246	3.837	0.0060
BRNI	0.94796	1.441	0.2257
URMO	0.93615	1.790	0.1362
LOFL	0.94698	1.470	0.2167
DIER	0.97991	0.538	0.7081
TIAM	0.98958	0.276	0.8927
IRBE	0.98911	0.289	0.8846
PADE	0.78292	7.278	0.0000
PACO	0.98196	0.482	0.7487
POSQ	0.96735	0.885	0.4752
SPPY	0.87654	3.697	0.0074
CHVI	0.95460	1.248	0.2951
SENI	0.98702	0.345	0.8469
SPAF	0.84465	4.828	0.0013
PEPA	0.98577	0.378	0.8233
ERCR	0.96716	0.891	0.4719
DISM	0.99005	0.263	0.9006

Appendix K

The standardized weights for 37 variables from a D.F.A. of 5 herbivore species.

Variable	DF1	DF2	DF3
% variance	49.61	26.45	13.94
COVER	0.091	0.308	-0.062
HEIGHT	0.565	-0.023	0.008
CYDA	-0.276	-0.470	-0.674
ARCO	0.132	-0.343	0.072
RHRE	0.249	-0.200	-0.055
HECO	-0.390	-0.119	-0.468
THTR	-0.288	-0.360	0.347
ERCU	-0.095	-0.367	-0.095
ERSU	-0.225	-0.278	-0.154
ERRI	-0.238	-0.306	-0.340
ERRA	-0.279	0.402	-0.259
ERPL	-0.408	0.265	0.426
ERGU	0.734	-0.001	0.289
ELAR	0.022	-0.167	-0.082
CYEX	-0.577	-0.152	-0.459
HYHI	0.282	-0.428	-0.183
TRGR	0.465	-0.269	0.077
BOIN	0.020	-0.069	-0.169
TRRE	-0.181	0.482	0.568
SEFL	0.015	0.048	0.017
BRSE	-0.349	0.028	-0.229
BRNI	-0.200	-0.010	0.030
URMO	-0.060	-0.226	-0.489
LOFL	0.254	-0.708	0.084
DIER	-0.141	-0.493	0.081
DIAM	-0.245	-0.138	-0.217
TRBE	-0.035	-0.164	-0.214
PADE	-0.727	-0.868	-0.019
PACO	0.161	-0.115	-0.295
POSQ	0.173	-0.105	0.226
SPPY	-0.142	-0.398	0.404
CHVI	0.265	0.098	0.483
SENI	0.036	-0.098	-0.063
SPAF	-0.199	0.283	0.388
PEPA	0.271	0.906	-0.139
ERCR	-0.328	-0.283	0.109
DISM	0.086	0.033	-0.174

Appendix L

(a) Secondary Grasslands:

	Late-wet	Late-dry
Late-wet	-	9.97**
Late-dry	-	-

(b) Pediment Grasslands:

	Late-wet	Late-dry
Late-wet	-	9.55**
Late-dry	-	-

(c) Valley Savannas:

	Late-wet	Late-dry
Late-wet	-	3.18*
Late-dry	-	-

(d) Thickets:

	Late-wet	Late-dry
Late-wet	-	7.83**
Late-dry	-	-

Table 3.3 : Results for Students' t-test comparing differences in above ground biomass for each season. (* = significant at the 5% level; ** = significant at the 1% level).

APPENDIX M

```
PROGRAM STOCKDENS (INPUT, OUTPUT);
(*==============*)


CONST M=5; A=1; E=5; NUMDAYS=91;


TYPE PRODRANGE = 1..E;
     PRODINDEX = 0..E;
     PRODRECORD = RECORD
                   PAL : REAL;
                   INT : REAL;
                  END;

     PRODARRAY = ARRAY [PRODRANGE] OF PRODRECORD;

     ANINDEX = 0..M;
     ANRANGE = 1..M;
     ANARRAY = ARRAY [PRODRANGE, ANRANGE] OF REAL;

     INITANARRAY = ARRAY [ANRANGE] OF REAL;

     COEFRANGE = 1..4;
     COEFINDEX = 0..4;


     COEFARRAY = ARRAY [PRODRANGE, ANRANGE, COEFRANGE] OF REAL;


     RAINRANGE = 1..4;

     CHARSET = SET OF CHAR;

     CONCOEFARRAY = ARRAY [ANRANGE] OF REAL;
     MINPLARRAY = ARRAY [ANRANGE] OF REAL;
     DISTARRAY = ARRAY [ANRANGE] OF REAL;


VAR PRINTOUT : TEXT;

    VEG : PRODARRAY;

    HABITAT : PRODINDEX;

    ANBIOM : ANARRAY;

    INITANBIO : INITANARRAY;

    DISTFILE : TEXT;

    AREA : ARRAY [PRODRANGE] OF INTEGER;
    PALTOINT, MAXPLBI : ARRAY [PRODRANGE] OF REAL;
    PREFPAL, CONCOEF : CONCOEFARRAY;

    INIDISTCOEF : COEFARRAY;

    MINPLBI : MINPLARRAY;

    MINRAIN, MAXRAIN : ARRAY [RAINRANGE] OF INTEGER;

    SEED, PERIOD, YEAR : INTEGER;

    SEASON : COEFINDEX;

    RAINFALL, PLPROD, SUMCONPAL, SUMCONINT : REAL;

    MINDIST : DISTARRAY;
```

```
    CHFIRE, QPRINT : CHAR;
    FIRE, NEGPLBIO, PALBOOL : BOOLEAN;



PROCEDURE READDATA;
(*--------------*)

 VAR I : PRODRANGE;
     J : ANRANGE;

 BEGIN

  FOR J := 1 TO M DO
   BEGIN

   WRITE ('INIT ANIM BIOM OF SP',J, '='); READLN (INITANBIO[J]);
   WRITELN;

   END;

  FOR I := A TO E DO
   BEGIN

   WRITE ('INIT PAL STAND CROP FOR HABITAT',I, '='); READLN (VEG[I].PAL);
   WRITE ('INIT INT STAND CROP FOR HABITAT',I, '='); READLN (VEG[I].INT);
   WRITELN;

   END;

  WRITE ('FIRE : YES(Y) OR NO(N)?'); READLN (CHFIRE);
  WRITE ('RANDOM INTEGER NUMBER='); READLN (SEED);
  WRITE ('PERIOD='); READLN (PERIOD);

END; (*READDATA*)



PROCEDURE CONSTANTS;
(*---------------*)

   GIN

  AREA[1]:=3120; AREA[2]:=1630; AREA[3]:=7320; AREA[4]:=23366;
  PALTOINT[1]:=0.45; PALTOINT[2]:=0.3; PALTOINT[3]:=0.5; PALTOINT[4]:=0.6;
  PALTOINT[5]:=0.6; PREFPAL[1]:=0.65; PREFPAL[2]:=0.4; PREFPAL[3]:=0.6;
  PREFPAL[4]:=0.7; PREFPAL[5]:=0.8; CONCOEF[1]:=0.25; CONCOEF[2]:=0.2;
  CONCOEF[3]:=0.2; CONCOEF[4]:=0.2; CONCOEF[5]:=0.15; MAXPLBI[1]:=13.1;
  MAXPLBI[2]:=12.1; MAXPLBI[3]:=46.8; MAXPLBI[4]:=173;
  MAXPLBI[5]:=30; MINRAIN[1]:=100; MINRAIN[2]:=150; MINRAIN[3]:=0;
  MINRAIN[4]:=0; MAXRAIN[1]:=400; MAXRAIN[2]:=600; MAXRAIN[3]:=100;
  MAXRAIN[4]:=40; AREA[5]:=7535; MINPLBI[1]:=2.5; MINPLBI[2]:=0.002;
  MINPLBI[3]:=0.0025; MINPLBI[4]:=0.003; MINPLBI[5]:=0.0035;

 END; (*CONSTANTS*)



FUNCTION RANDOM (VAR SEED : INTEGER) : REAL;
(*-----------*)

CONST DIVISOR = 32767;

 BEGIN


  (* $R- *)
```

```
   SEED := (25173 * SEED + 13849) MOD DIVISOR;

  (* $R+ *)

   SEED := ABS (SEED);

   RANDOM := SEED / DIVISOR;

 END; (*RANDOM*)


PROCEDURE READCOEF (VAR INIDISTCOEF : COEFARRAY);
(*--------------*)

VAR I : PRODRANGE;
    J : ANRANGE;
    SEASON : COEFRANGE;

BEGIN

 FOR I := A TO E DO
  FOR J := 1 TO M DO
   FOR SEASON := 1 TO 4 DO
    BEGIN
     READ (DISTFILE, INIDISTCOEF[I,J,SEASON]);
    END;

 END; (*READCOEF*)


 PROCEDURE READCH (MARKSET : CHARSET; VAR CH : CHAR);
 (*------------*)

 BEGIN
  REPEAT
   READ (CH);

    IF (CH IN MARKSET) THEN WRITE (CH) ELSE
     WRITE (CHR(7));

  UNTIL (CH IN MARKSET);

 END; (*READCH*)


PROCEDURE SEASONLOOP (DISTCOEF : COEFARRAY);
(*----------------*)

 VAR SPECIES : ANRANGE;
     NEGSPECIES : ANINDEX;
     CONPAL, CONINT : REAL;
     DISTLIMIT : ANRANGE;

PROCEDURE PLANTBIOM (RAINFALL : REAL; VAR VEG : PRODARRAY);
(*---------------*)


 VAR PROD : PRODARRAY;
     PLRAIN : REAL;
     I : PRODRANGE;


PROCEDURE PRODUCTION (PLRAIN, PALTOINT, VEGPAL, VEGINT, MAXPLBI : REAL;
 (*----------------*)    AREA : INTEGER; VAR PLPROD, PRODPAL,
                        PRODINT : REAL);
```

```
   BEGIN

    PLPROD := PLRAIN * AREA * (1 - ((VEGPAL + VEGINT) / MAXPLBI))
              /(PWROFTEN(6));

    PRODPAL := PLPROD * PALTOINT;
    PRODINT := PLPROD - PRODPAL;

   END; (*PRODUCTION*)


 PROCEDURE VEGETATION (PRODPAL, PRODINT : REAL; VAR VEGPAL,
 (*-----------------*)  VEGINT : REAL);


  BEGIN

   VEGPAL := VEGPAL + PRODPAL;
   VEGINT := VEGINT + PRODINT;

  END; (*VEGETATION*)


 BEGIN (*PLANTBIOM*)


  IF RAINFALL > 21 THEN
   PLRAIN := -113 + 5.48 * RAINFALL
  ELSE
   PLRAIN := 10;

   FOR I := A TO E DO
    BEGIN

    PRODUCTION (PLRAIN, PALTOINT[I], VEG[I].PAL, VEG[I].INT, MAXPLBI[I],
                 AREA[I], PLPROD, PROD[I].PAL, PROD[I].INT);

    VEGETATION (PROD[I].PAL, PROD[I].INT, VEG[I].PAL, VEG[I].INT);

    END;

 END; (*PLANTBIOM*)



PROCEDURE ANIMCONS (ANBIOM, CONCOEF, PREFPAL : REAL;
(*---------------*)  VAR CONPAL, CONINT : REAL);

 VAR CONSUMP : REAL;

  BEGIN
   CONSUMP := ANBIOM * CONCOEF * NUMDAYS;

    CONPAL := CONSUMP * PREFPAL;
    CONINT := CONSUMP * (1 - PREFPAL);
  END; (*ANIMCONS*)


PROCEDURE VEGCONS (DISTCOEF : COEFARRAY; INITANBIO : INITANARRAY);
(*--------------*)


 VAR J : ANRANGE:
```

```
PROCEDURE HEADING;
(*---------------*)

 VAR I : ANRANGE;

  BEGIN

   WRITELN (PRINTOUT); WRITELN (PRINTOUT);
   WRITELN (PRINTOUT, ' ':4, 'YEAR = ',YEAR:1, ' ':10, 'SEASON = ',
            SEASON:1, ' ':10, 'RAINFALL = ', RAINFALL:7:1);
   WRITELN (PRINTOUT); WRITELN (PRINTOUT);
   WRITELN (PRINTOUT, ' ':30, 'ANIMAL BIOMASS:');
   WRITELN (PRINTOUT, ' ':30, '===============');
   WRITELN (PRINTOUT);
   WRITE (PRINTOUT, ' ':14);
    FOR I := 1 TO M DO
     WRITE (PRINTOUT, ' SPECIES ',I:1,' ':2);
   WRITELN (PRINTOUT);

  END; (*HEADING*)


  PROCEDURE ANIMTABLE (HABITAT : PRODINDEX; ANBIOM : ANARRAY);

  VAR I : PRODRANGE;
      J : ANRANGE;

  BEGIN

   FOR I := A TO E DO
    BEGIN
     WRITE (PRINTOUT, 'HABITAT',I : 1);
     FOR J := 1 TO M DO
      BEGIN
       WRITE (PRINTOUT, ANBIOM[I,J]:10:4,' ':4);
      END;

     WRITELN (PRINTOUT);

    END;
  END;


PROCEDURE PLANTTABLE (VEG : PRODARRAY);
(*----------------*)

 VAR I : PRODRANGE;

  BEGIN

   WRITELN (PRINTOUT);
   WRITELN (PRINTOUT, ' ':30, 'PLANT BIOMASS:');
   WRITELN (PRINTOUT, ' ':30, '==============');
   WRITELN (PRINTOUT);
   WRITE (PRINTOUT, ' ':14);
    FOR I := A TO E DO
     WRITE (PRINTOUT, ' HABITAT ',I:1,' ':2);
     WRITELN (PRINTOUT);

   WRITE (PRINTOUT, ' PALATABLE    ');
    FOR I := A TO E DO
     WRITE (PRINTOUT, VEG[I].PAL:10:4, ' ':2);
   WRITELN (PRINTOUT);
   WRITE (PRINTOUT, ' INTERMEDIATE ');
    FOR I := A TO E DO
     WRITE (PRINTOUT, VEG[I].INT:10:4, ' ':2);
```

```
    WRITELN (PRINTOUT);

   END; (*PLANTTABLE*)


  BEGIN (*VEGCONS*)

   HEADING;


    HABITAT := 0;

     REPEAT
      HABITAT := HABITAT + 1;

      SUMCONPAL := 0; SUMCONINT := 0;

     FOR J := 1 TO M DO
      BEGIN

       WRITELN (PRINTOUT, 'DISTCOEF=', DISTCOEF[HABITAT,J,SEASON]);

       ANBIOM[HABITAT,J] := INITANBIO[J] * DISTCOEF[HABITAT,J,SEASON];

      ANIMCONS (ANBIOM[HABITAT,J], CONCOEF[J], PREFPAL[J],
                CONPAL, CONINT);

       SUMCONPAL := SUMCONPAL + CONPAL;
       SUMCONINT := SUMCONINT + CONINT;

      END;

       VEG[HABITAT].PAL := VEG[HABITAT].PAL - SUMCONPAL;
       VEG[HABITAT].INT := VEG[HABITAT].INT - SUMCONINT;

       WRITELN (PRINTOUT, 'SUMCONPAL=',SUMCONPAL,'SUMCONINT=',SUMCONINT);

       NEGSPECIES := 0;
        REPEAT
        NEGSPECIES := NEGSPECIES + 1;
         NEGPLBIO := (VEG[HABITAT].PAL < (MINPLBI[NEGSPECIES] *
                     PREFPAL[NEGSPECIES])) OR
                     (VEG[HABITAT].INT < (MINPLBI[NEGSPECIES] * (1 -
                     PREFPAL[NEGSPECIES])));
        UNTIL (NEGSPECIES >= M) OR NEGPLBIO;

     UNTIL (HABITAT >= E) OR NEGPLBIO;

    IF NOT NEGPLBIO THEN
     BEGIN
      ANIMTABLE (HABITAT,ANBIOM);
      PLANTTABLE (VEG);
     END
     ELSE
      BEGIN
      VEG[HABITAT].PAL := VEG[HABITAT].PAL + SUMCONPAL;
      VEG[HABITAT].INT := VEG[HABITAT].INT + SUMCONINT;
      END;

  END; (*VEGCONS*)



PROCEDURE MODMINDIST (VEG : PRODARRAY; MINPLBI : MINPLARRAY;
(*-----------------*)  INITANBIO : INITANARRAY; PLPROD : REAL;
                       VAR MINDIST : DISTARRAY);

 VAR PLBITEMP, PLBION, PLBIOFF, TEMPPLBION, CONPAL, CONINT : REAL;
     HERB : ANINDEX;
```

```
FUNCTION SUMINIT (INIDISTCOEF : COEFARRAY) : REAL;

 VAR J : ANRANGE;
     SUM : REAL;

 BEGIN
  FOR J := 1 TO M DO
   IF J <> NEGSPECIES THEN
    SUM := SUM + INIDISTCOEF[HABITAT,J,SEASON];
    SUMINIT := SUM
 END; (*SUMINIT*)



BEGIN (*MODMINDIST*)


ANIMCONS (ANBIOM[HABITAT,NEGSPECIES], CONCOEF[NEGSPECIES],
         PREFPAL[NEGSPECIES], CONPAL, CONINT);


PALBOOL := FALSE;

   (VEG[HABITAT].PAL-SUMCONPAL) < (MINPLBI[NEGSPECIES] *
   PREFPAL[NEGSPECIES]) THEN
   BEGIN
    PALBOOL := TRUE;
    PLBITEMP := VEG[HABITAT].PAL - SUMCONPAL;
   END
 ELSE
IF (VEG[HABITAT].INT-SUMCONINT) < (MINPLBI[NEGSPECIES] *
       (1 - PREFPAL[NEGSPECIES])) THEN
   PLBITEMP := VEG[HABITAT].INT - SUMCONINT;

IF PLBITEMP < 0 THEN
 PLBIOFF := ABS(PLBITEMP) + MINPLBI[NEGSPECIES]
ELSE
 PLBIOFF := MINPLBI[NEGSPECIES] - PLBITEMP;

IF (PLBIOFF > CONPAL) OR (PLBIOFF > CONINT) THEN
 BEGIN
  DISTLIMIT := M;
  MINDIST[NEGSPECIES] := 0;

   IF PALBOOL = TRUE THEN
    TEMPPLBION := VEG[HABITAT].PAL - (MINPLBI[NEGSPECIES] *
                  PREFPAL[NEGSPECIES]) ELSE
    TEMPPLBION := VEG[HABITAT].INT - (MINPLBI[NEGSPECIES] *
                 (1 - PREFPAL[NEGSPECIES]));

   HERB:= 0;
  REPEAT
   HERB:= HERB + 1;
   IF NOT (HERB = NEGSPECIES) THEN

   MINDIST[HERB] := ((TEMPPLBION * (INIDISTCOEF[HABITAT,HERB,
                                                SEASON] /
                      SUMINIT(INIDISTCOEF))) / (CONCOEF[HERB] * 91)) /
                      INITANBIO[HERB];
   WRITELN (PRINTOUT, 'MINDIST=',MINDIST[HERB]);
  UNTIL HERB >= M;
 END
 ELSE BEGIN
  IF PALBOOL = TRUE THEN
   PLBION := CONPAL - PLBIOFF
  ELSE BEGIN
   PLBION := CONINT - PLBIOFF;
   MINDIST[NEGSPECIES] := ((PLBION / CONCOEF[NEGSPECIES]) * 91) /
                          INITANBIO[NEGSPECIES];
```

```
    DISTLIMIT := 1;
    WRITELN (PRINTOUT, 'MINDIST=',MINDIST[NEGSPECIES]);
   END;
  END;

 END; (*MODMINDIST*)



PROCEDURE MODDIST (MINDIST : DISTARRAY; INIDISTCOEF : COEFARRAY;
(*-------------*)  VAR DISTCOEF : COEFARRAY);

 VAR HAB : PRODINDEX;
     TEMPCOEF, DIFFDIST : REAL;
     TEMPSPECIES : ANRANGE;


 PROCEDURE UPDATEDIST (MINDIST : DISTARRAY; INIDISTCOEF : COEFARRAY;
 (*----------------*) VAR DISTCOEF : COEFARRAY;
                      VAR DIFFDIST : REAL);


  VAR SPECIES : ANRANGE;

  BEGIN

       DIFFDIST := INIDISTCOEF[HABITAT,TEMPSPECIES,SEASON] -
                   MINDIST[TEMPSPECIES];
       DISTCOEF[HABITAT,TEMPSPECIES,SEASON] := MINDIST[TEMPSPECIES];
  WRITELN (PRINTOUT, 'MODDIST1=',DISTCOEF[HABITAT,TEMPSPECIES,SEASON]);

  END; (*UPDATEDIST*)



FUNCTION SUMHAB (HABITAT : PRODINDEX; SPECIES : ANINDEX) : REAL;
(*------------*)

 VAR I : PRODRANGE;
     SUM : REAL;


 BEGIN

  SUM := 0;

  FOR I := 1 TO E DO
   IF I <> HABITAT THEN
    SUM := SUM + INIDISTCOEF[I,SPECIES,SEASON];
    SUMHAB := SUM;

 END; (*SUMHAB*)



 BEGIN (*MODDIST*)

 FOR SPECIES := 1 TO DISTLIMIT DO
 BEGIN
  IF DISTLIMIT = 1 THEN TEMPSPECIES := NEGSPECIES
  ELSE TEMPSPECIES := SPECIES;

  UPDATEDIST (MINDIST, INIDISTCOEF, DISTCOEF, DIFFDIST);

   HAB := 0;

   REPEAT
```

```
   HAB := HAB + 1;

   IF NOT (HAB = HABITAT) THEN
    BEGIN

      TEMPCOEF := (INIDISTCOEF[HAB,TEMPSPECIES,SEASON] *
                                       DIFFDIST) /
                                       SUMHAB(HABITAT,TEMPSPECIES);

      DISTCOEF[HAB,TEMPSPECIES,SEASON] := TEMPCOEF + INIDISTCOEF[HAB,
                                       TEMPSPECIES,SEASON];
      WRITELN (PRINTOUT, 'MODDIST2=',DISTCOEF[HAB,TEMPSPECIES,SEASON]);

     END;

  UNTIL HAB = E;

  END;

END; (*MODDIST*)

 BEGIN (*SEASONLOOP*)

  SEASON := 0;

  NEGPLBIO := FALSE;

  REPEAT

   SEASON := SEASON + 1;

    IF NOT NEGPLBIO THEN

    RAINFALL := MINRAIN[SEASON] + (MAXRAIN[SEASON] - MINRAIN[SEASON])
                * RANDOM(SEED);

   PLANTBIOM (RAINFALL, VEG);
   VEGCONS (DISTCOEF, INITANBIO);

    IF NEGPLBIO THEN BEGIN
     MODMINDIST (VEG, MINPLBI, INITANBIO, PLPROD, MINDIST);
     MODDIST (MINDIST, INIDISTCOEF, DISTCOEF);

     SEASON := SEASON - 1;
    END;

  UNTIL SEASON >= 4;

 END; (*SEASONLOOP*)



 (*MAIN PROGRAM FOLLOWS*)


 BEGIN


  WRITE (' PRINTED COPY ? (Y/N) '); READLN (QPRINT);

   IF QPRINT = 'Y' THEN
    REWRITE (PRINTOUT, 'PRINTER:')
     ELSE
    REWRITE (PRINTOUT, 'CONSOLE:');

  WRITELN (PRINTOUT);
```

```
 WRITELN (' INSERT DISK WITH DISTDATA FILE(S) THEN TYPE SPACE: ');

 READCH([' '],QPRINT);

 RESET (DISTFILE, 'DISTDATA.DATA');

 READDATA;
 CONSTANTS;
 READCOEF (INIDISTCOEF);


  YEAR := 0;

  REPEAT

   YEAR := YEAR + 1;

   SEASONLOOP (INIDISTCOEF);

  UNTIL YEAR >= PERIOD;

 CLOSE (DISTFILE, LOCK);

END. (*MAIN PROGRAM*)
```

APPENDIX N

The Carrying Capacity stocking rates for the Bulk and Concentrate grazers (impala included) as recommended by Collinson and Goodman (1981) for the Pilanesberg Game Reserve.

Estimated flat projected area = 49000 ha.
Estimated carrying capacity = 1AU to 15 ha.
Total permissible animal units = 3264

Species	Feeding class	Recommanded animal units	Recommended numbers	Number introduced	Current status	AU equivalents
White rhino	1	488	200	250	± 250	0.41
Buffalo	1	446	450	11	12	1.01
Roan	1	97	170	0	0	1.73
Zebra	1	269	500	679	±1000	1.86
Sable	1	102	200	13	14	1.97
Waterbuck	1	68	150	60	40	2.19
Wildebeest	2	187	400	824	±1500	2.14
Gemsbuck	2	43	100	158	155	2.30
Hartebeest	2	249	650	901	±1500	2.64
Tsessebe	2	69	200	7	8	2.91
Common reedbuck	2	38	200	0	0	5.25
Mountain reedbuck	2	49	400	0	numerous	8.11
Warthog	2	18	100	0	numerous	5.68
Impala	3	160	1000	1909	±3500	6.20

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Professor K.H. Rogers,
Wits University, Botany Department
Private Bag 3
Wits 2050